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# COLOUR PATTERNS OF THE DWARF MINKE WHALE *BALAENOPTERA ACUTOROSTRATA* SENSU LATO: DESCRIPTION, CLADISTIC ANALYSIS AND TAXONOMIC IMPLICATIONS

PETER W. ARNOLD, R. ALASTAIR BIRTLES, ANDY DUNSTAN, VIMOKSALEHI LUKOSCHEK AND MONIQUE MATTHEWS

Arnold, P.W., Birtles, R.A., Dunstan, A., Lukoschek, V. & Matthews, M. 2005 12 31: Colour patterns of the dwarf minke whale *Balaenoptera acutorostrata* sensu lato: description, cladistic analysis and taxonomic implications. *Memoirs of the Queensland Museum* **51**(2): 277-307. Brisbane. ISSN 0079-8835.

Colour patterns of the dwarf minke whale, the most complex of any baleen whale, are described and illustrated. While variability is sufficient to allow recognition of individual whales, distinct colour elements consistently occur, including a light grey rostral saddle, dark grey spinal field and ivory white ventral field. Three dark lateral fields (nape field, continuing ventrally as a throat patch; thorax field; pedunele field) alternate with light grey thorax and flank patches and ivory white peduncle and shoulder blazes, the last variably in-filled by a dark axillary patch. The flipper has a diagnostic white basal blaze and dark grey distal patch. White mandible and eye blazes occur primarily on the right side.

Cladistic analyses were run using 13 colour characters and 12 taxa (11 baleen whales, representing all families; outgroup: sperm whale *Physeter*). The relationships between baleen whale families were poorly reflected in the analysis and no monophyletic groups were extracted. However the analysis suggested that the common minke whale *Balaenoptera acutorostrata* and the dwarf minke whale are most closely related. The common minke , dwarf minke and Antarctic minke whale *Balaenoptera bonaerensis* were also united, as only those species shared a double caudal chevron and discrete light grey lateral patches (anterior thorax and posterior flank patch) separated by a dark thorax field. Light grey lateral pigment, blowhole streaks, ear stripes and a tendency for colour asymmetry characterised most species of *Balaenoptera*. Colour pattern and other available data support Rice's (1998) recognition of the dwarf minke whale as an as yet un-named subspecies of *Balaenoptera acutorostrata*. ☐ *Cetacea, Balaenopteridae, colouration, phylogeny, taxonomy.*

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Until quite recently, the minke whale was considered to be a single species with one of the most extensive cetacean distributions (Stewart & Leatherwood, 1985). Rice (1998) summarized the morphological, osteological and genetic data and suggested that two species be recognised: the 'common' minke whale *Balaenoptera acutorostrata* (Lacépède, 1804) and the 'Antarctic' minke whale *Balaenoptera bonaerensis* Burmeister, 1867. A review by the Scientific Committee of the International Whaling Commission (IWC, 2001) accepted the recognition of these two species, but deferred a decision on other nominal taxa, including a diminutive or dwarf form (Best, 1985; Arnold et al., 1987; Zerbini et al., 1996) found throughout the Southern Hemisphere, pending a world-wide review of morphological and molecular data.

As part of this general re-evaluation, we present data on colour patterns of the dwarf minke whale, based primarily on field observations. Best (1985) noted several diagnostic features: a dark throat patch, 'Type 3' flipper with dark tip and white base, and a white shoulder patch. He discussed several other colour features in comparison with the Antarctic minke whale. Based primarily on presence of a dark throat patch or Type 3 flipper, he also documented the diminutive form from eastern Australia, New Zealand and Brazil.

External characters, such as colouration, are amenable to field studies and, as with birds, field

observations can provide data based on a relatively large sample size (Corbet, 1997). We have recognised over 200 dwarf minke whales on the northern Great Barrier Reef during 1999-2001. We have detailed field colour notes for about 100 individuals in each of 1999 and 2000. We also review photographs from Australia, the South Pacific, New Zealand and Brazil.

With this new information on the colour pattern variation in dwarf minke whales, we compare colour patterns in Antarctic minke whales (Best, 1985; Bushuev & Ivashin, 1986), common minke whales and other mysticetes. We attempt to establish which colour patterns are homologous and establish a consistent terminology for the features. This allows a better documentation of colour pattern details, which are used to recognise individual whales in photo- and/or video-ID studies, as well as discussion of features of possible phylogenetic significance. Colour patterns have been used to assess taxonomic and/or phylogenetic relationships in odontocetes (Mitchell, 1970; Perrin, 1997) but we know of no similar attempts for mysticetes.

## MATERIALS AND METHODS

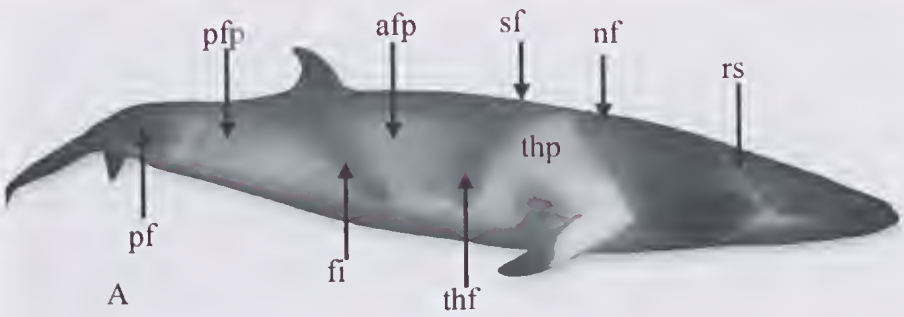
Dwarf minke whales were observed primarily from the dive vessel *Undersea Explorer* as part of a wider study, conducted since 1996, on the biology and behaviour of the whales and management of swimmer-whale interactions during commercial swim-with-whale activities (Birtles et al., 2002; Valentine et al., 2004). Observations of colour pattern were made both from the surface and underwater but rely primarily on the latter, representing over 200 individuals in 1999-2001. Colour patterns, as well as scar patterns, have been used to recognise individual whales. The photo- and video-IDs are being used to document within-season and between year re-sightings (Birtles et al., 2002), which in turn provide information on spatial and temporal distributions of the whales, site fidelity, association patterns and potential for cumulative impacts.

The greatest resolution is obtained from still images; such images, primarily from the field seasons 1999-2002, are used for the illustrations in this paper. Underwater video was routinely used for identification of individuals by colour and scar patterns; it also provided documentation of colour pattern variations. Video was an especially effective tool because (1) it documented animals from different angles so that we could confirm that a lighter feature was actually a colour pattern rather than a reflection of light; (2) it provided clear indications of whether the animal was observed from the right or left sides, and (3) a sequence could contain views of both right and left sides of an individual, allowing matching of the asymmetrical colour patterns. Still images could be extracted from digital video using "DVD Tools". Underwater field colour notes (mainly by RAB) could also be used to assess colour patterns of individuals and could be matched to particular video sequences.

Published and unpublished photographs and video submitted by divers, commercial photographers and scientific colleagues were also examined. These represent an additional 15 animals from Queensland (Arnold et al., 1987: 10; Paterson, 1994: 1; unpublished Queensland Museum records: 4); one from Marion Reef, Coral Sea (Rockman, 1986 a, b); two from New South Wales ( Arnold et al., 1987: 1; Australian Museum archives: 1); two from Victoria (Arnold et al., 1987), one from New Caledonia (Laboute & Magnier, 1979), one from Vanuatu (video), 3 from New Zealand (Baker, 1983: 1; unpublished from S. Gibney: 2), one from Fiji (email images from C. Holloway) and 3 from Brazil (Secchi et al., 2003:1; 2 unpublished, from A. Zerbini).

Although it is possible to reverse images on video, this is usually done only by commercial producers who have the appropriate editing facilities. Videos showing a particular side of an animal could therefore be accepted as valid documentation. More care is needed with photographs. We have found transparencies mounted inaccurately but such cases can be checked easily. More problems occur when working from copies of original transparencies, when such sheets on the film may not resolve any ambiguity in orientation of the whale. In such cases, we have used a combination of features such as the orientation of the blowhole streaks, posterior extension and shape of the rostral saddle, and extent of white blazes on the mandible and around the eye (see below). Direct observations and analysis of unedited video have shown that such features are consistently asymmetrical and can be used to determine which side the photograph shows.

This paper depends on photographs to document variation in particular features. For the dwarf minke whale, we include a number of previously unpublished images. Adobe Photoshop was used to remove the background from the underwater photographs and to match



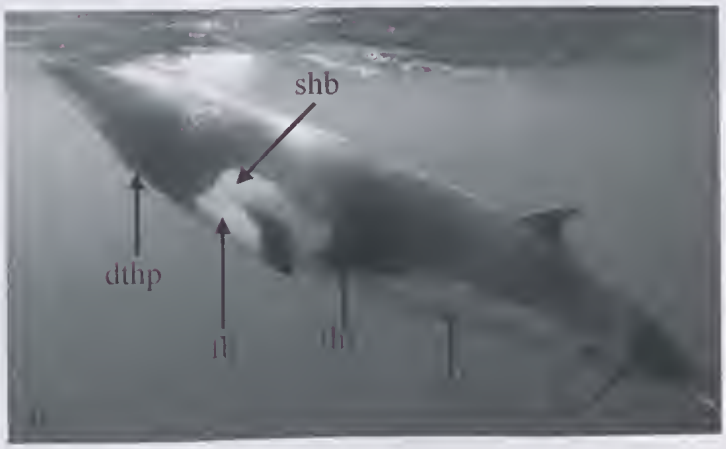
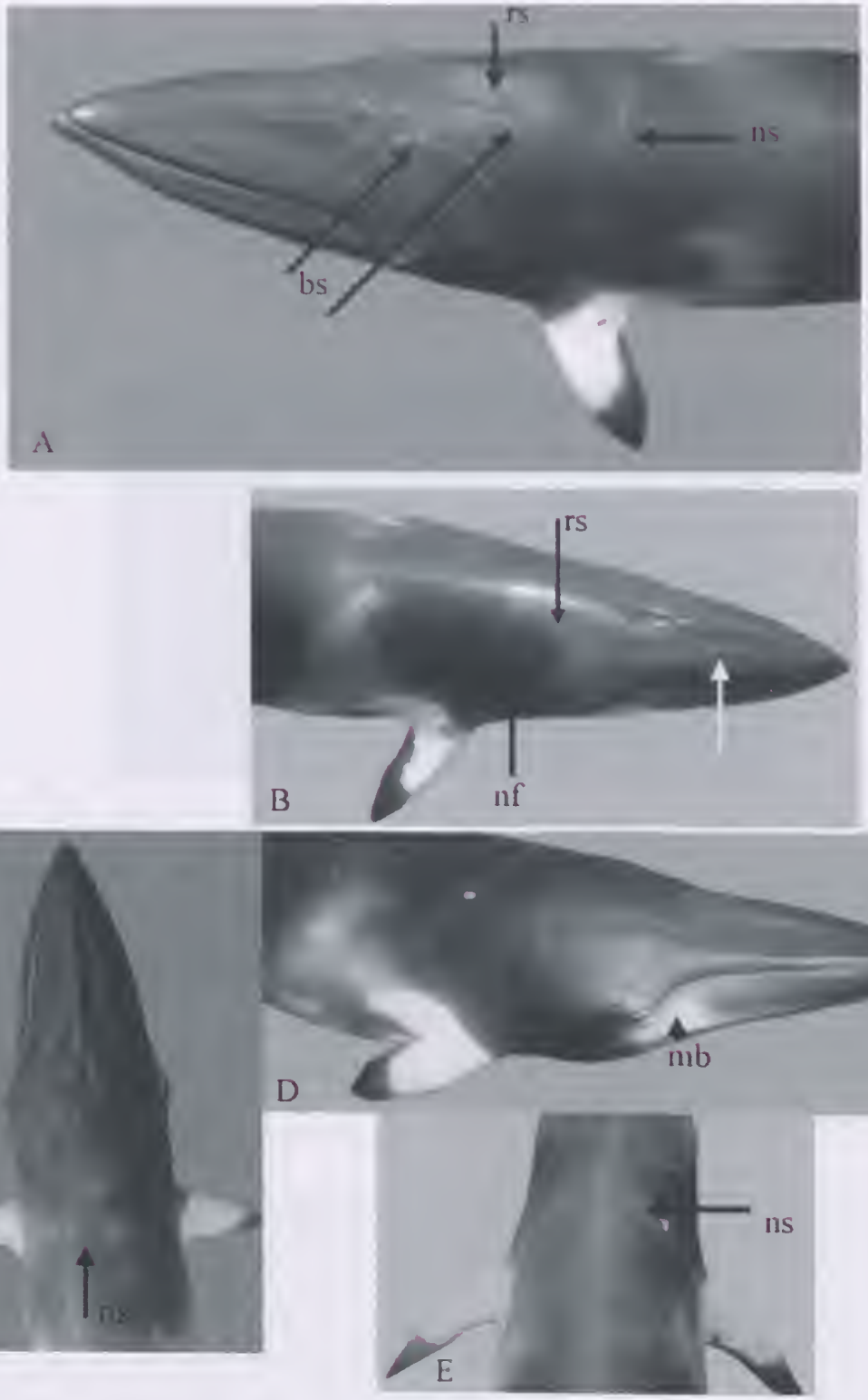



FIG. 1. Colour elements of the dwarf minke whale. A, Right lateral view, showing light rostral saddle (rs) and dark grey spinal field (sf) along the back; overall dark nape field (nf), thorax field (thf) and peduncle field (pf), with alternating light grey thorax patch (thp) anteriorly and flank patch posteriorly, the latter divided by a dark flank infill (fi) into an anterior flank patch (afp) and posterior flank patch (pfp). B, Left lateral view showing white ventral field (vf): dark throat patch (dthp), an extension of the nape field; dark thorax field (thf); double caudal chevron (cc); ivory white basal flipper blaze (fb) and shoulder blaze (shb). C, Ventro-lateral view showing ivory white ventral field; dark throat patch (dthp), and double caudal chevron (cc), bounding the peduncle blaze (pb). Note also the thin anterior extension of the flank infill (fi), as a fine swirl, in the form of a Salvador Dali moustache. The underside of the tail flukes is in shadow and appears dark; most of the underside of the flukes is actually ivory white, as on the ventral field, with a dark grey trim at the tips of the flukes and onto the trailing edge of the flukes.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the contrast in the black and white photographs to that in the colour originals (i.e. to ensure that the contrast of dark and light grey areas were not enhanced). References are given to published illustrations to either illustrate another variation or, more usually, to establish the generality of the pattern.

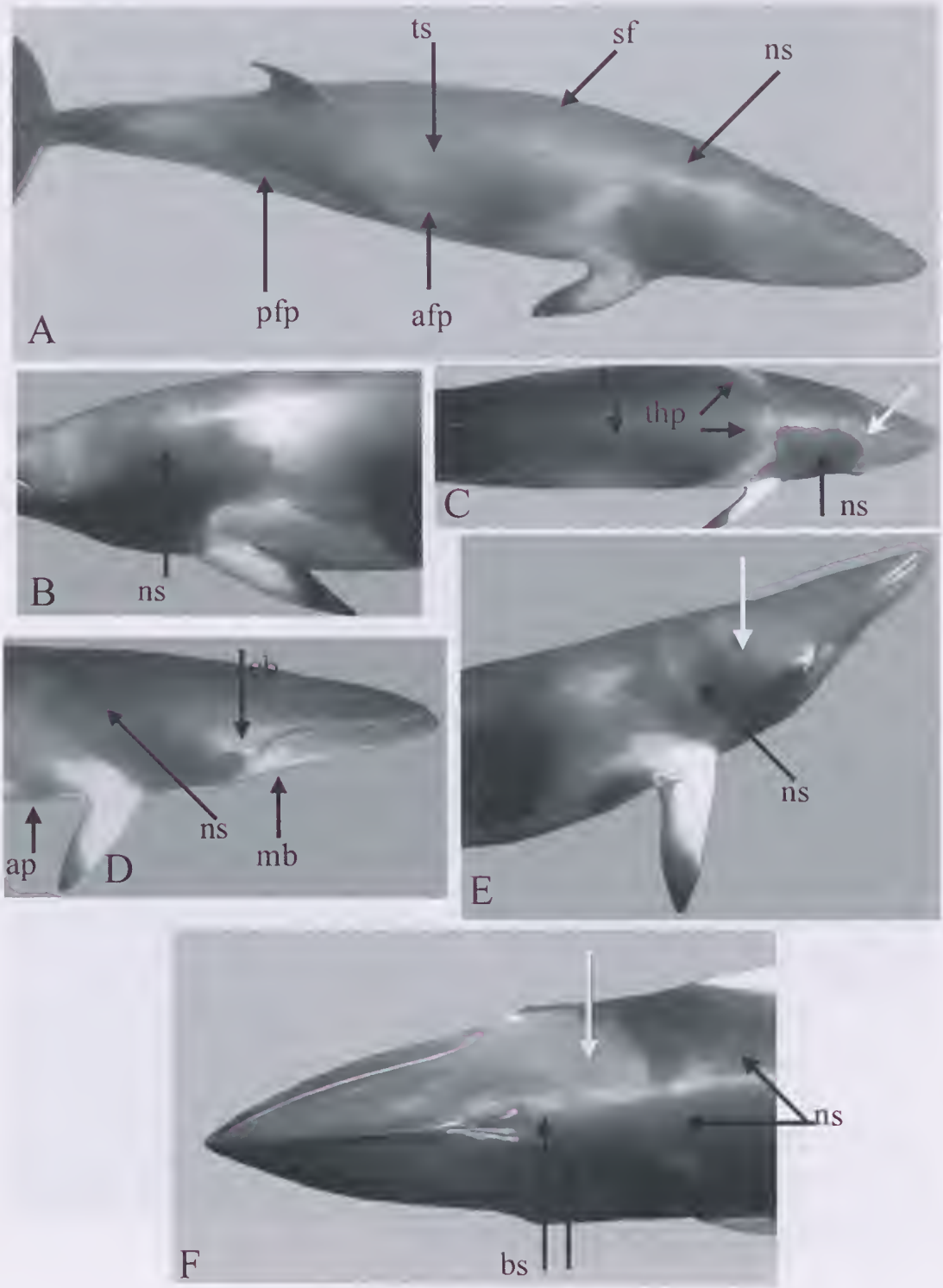
We rely largely on published descriptions and images for other mysticete species. Only photographs are used as evidence; although there are some excellent paintings (e.g. Foster in Leatherwood & Reeves, 1983) most illustrations of rorquals appear to be overly diagrammatic. This appears to be particularly true in illustrations of the common minke whale, and applies even to the most recent field guides (e.g. Folkens et al., 2002). Photographs of stranded whales may be from angles which obscure some of the colour patterns and often suffer from post-mortem darkening. Surface photos used for photo-ID's are especially valuable, but they show only the upper back of the animal. Underwater photographs are potentially the most useful but colour patterns may be obscured through extreme wave-refracted light creating dappling effects on the whales (e.g. sei and minke whales in Williamson, 1972, pls 1-3), through loss of contrast (e.g. fin whale in Cousteau, 1972: 50-51), or from angle of the shot (fin whale in Clapham, 1997: 46). There are additional problems with identification of the species in some publications (e.g. the photograph of a 'finback' whale in Cousteau (1972: 48) appears to be a Bryde's whale). The end result is that the documentation of particular colour elements may be based on photographs of a very small number of individuals. Within *Balaenoptera*, this is particularly the case for the Bryde's whale species complex and *B. omurai* Wada et al., 2003. While the appearance of a colour element in a photograph can be adequate proof for its existence in a particular species, failure to find it in photographs does not necessarily mean it is absent. It is thus difficult to generalise about colour elements in several species, a point that needs to be remembered when discussing phylogenetic significance of colour patterns.

The phylogenetic analyses were run using PAUP v. 4.0b10. Colour coding for the dwarf minke whale is based on new observations documented herein and a review of the literature. Colour coding for other species is based on the literature (Appendix). Insufficient information on the Bryde's whale complex or *B. omurai* was available to include any representative in the analyses. An exhaustive search was conducted. *Physeter* was set as the outgroup, based on phylogenies (Messenger & McGuire, 1998; Nikaido et al., 2001) which place the physeterids as a basal odontocete group.

## COLOUR PATTERN OF DWARF MINKE WHALE

The dwarf minke whale has a dark grey back and ivory white underside (ventral field). The lateral colouration is much more complex with three dark grey fields descending from the back, white blazes ascending from the ventral field and a series of light grey patches, saddles and streaks. Together, these constitute the most complex colouration in any mysticete. The various colour

FIG. 2 (facing). Dorsal colour elements. A, The light grey of the rostral saddle (rs) extends further posteriorly on the right side of the body and is better defined than on the left. The two light grey blowhole streaks (bs) are clearly defined; the left blowhole streak curves to the left, a consistent feature in dwarf minke whales. The thin dorsal portion of the nape streak (ns) extends further forward on the left side of the body. B, The posterior edge of the right rostral saddle (rs) is markedly concave or scalloped by an antero-lateral extension of the dark nape field (nf). The white arrow points to a lateral ridge on the right side of the upper jaw. Lateral rostral ridges have been considered a feature of Bryde's whales but occur in some individual dwarf minke whales. C, The complex contour of a nape streak (ns) is seen in this whale; the nape streak expands into a diffuse patch on the left side of the animal. Note also the left curve of the left blowhole streak, the more posterior extension of the right rostral saddle and two lateral ridges (one on either side of the median rostral ridge). D, The posterior margin of the right rostral saddle is convex, a dark chain-like scar runs through the middle of the right rostral saddle. The nape streak continues onto the side as a thin convex line, mirroring the smooth curve of the anterior margin of the light grey thorax patch. The white of the ventral field extends upwards onto the base of the lower jaw as a mandible blaze(mb); the anterior half of the eyelids is also white, forming an eye blaze. E, The thin transverse nape streak (ns) angles back sharply before continuing down the side of the body. There is a healing oval scar on the nape streak.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elements are detailed below, progressing from the head posteriorly.

DARK FIELDS. *Spinal field (sf).* This dark grey field on the dorsal surface (Figs 1A, 3A) overlays the occipital region of the skull and the whole vertebral column; it is called the spinal field, as in delphinids (e.g. Mitchell, 1970). It extends furthest forward along the midline of the back, just posterior to the blowholes, where it usually forms a dark background to the blowhole streaks (Fig. 3F; Clapham, 1997:60; Chadwick & Nicklin, 2001: 61). The spinal field extends downward on either side of the body as (1) a nape field continuing ventrally as a dark throat patch, (2) thorax field and (3) peduncle field (see below for details). It is usually at its narrowest above the flank patch just in front of and just behind the dorsal fin (Figs 3A,6B).

*Nape field (nf).* This dark band descends from the spinal field and continues ventrally as the dark throat patch. It is bordered anteriorly by the light grey rostral saddle, and posteriorly by the light grey thorax patch and white shoulder blaze (Figs 2B, 2D, 3B, 3D, 5A, 6B; Paterson, 1994, fig 2, lower; Hoelzel & Stern, 2000: 14, 26; Chadwick & Nicklin, 2001: 58-59).

*Dark throat patch (dthp).* All dwarf minke whales had a dark extension of the nape field extending onto the throat region from under the level of the eye to the anterior insertion of the flipper (Figs 1B, 1C, 5A, 7; Arnold et al., 1987, fig. 3a,e). It is particularly obvious when the throat is expanded. The development of the throat patch was asymmetrical on some individuals, extending further ventrally on the left side, but is not consistently so.

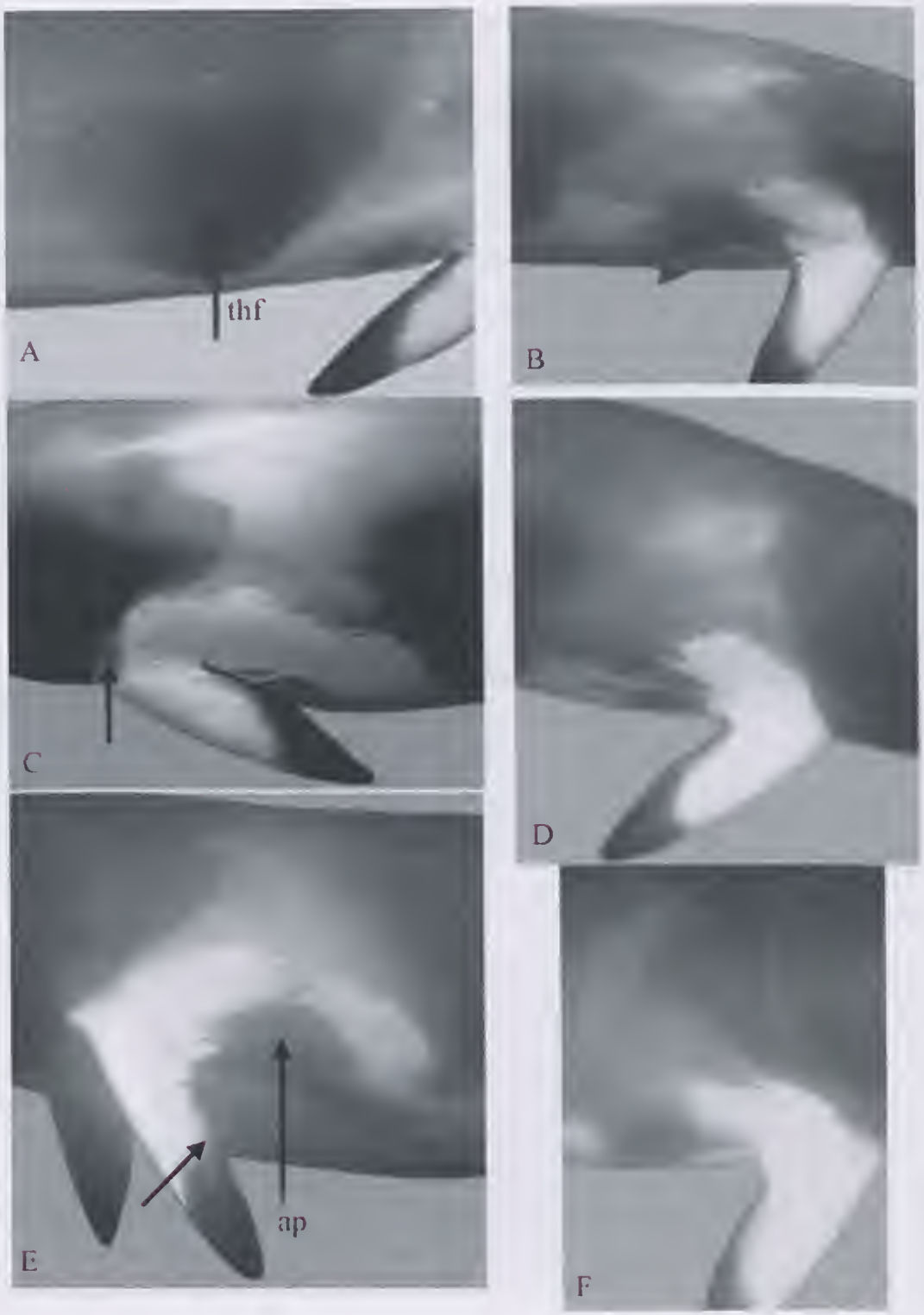
*Thorax field (thf).* This cape-like field descends from the spinal field and usually forms an inverted triangle, although in some individuals it is very narrow and vertically elongate. It is bordered anteriorly by the light grey thorax patch and posteriorly by the more variable, but generally light grey coloured flank patch. It may be a broad triangle with a truncated (Fig. 5C) or broadly rounded ventral margin (Figs 1C,3E), or thin with a more acute tip (Fig. 1A, 3A). The ventral margin of the thorax field may form an anteriorly directed hook (Fig. 1B); very occasionally the margin is bifurcated with both an anteriorly and a posteriorly directed hook.

*Peduncle field (pf).* Posterior to the flank patch and extending to the insertion of the flukes is a dark grey field which extends over all of the sides of the peduncle and well onto the ventral keel of the peduncle (Figs 1A, 3A, 5A).

*Caudal chevrons (cc).* The anterior margin of the peduncle field descends vertically onto the ventral field, then angles sharply forward, forming the posterior caudal chevron. The anterior caudal chevron, similarly angled, is a dark overlay extending from the flank patch onto the ventral field (Fig. 1B, C; Arnold et al., 1987, fig. 3e). In a few cases, the ventral portion of the chevrons may be detached from flank patch (*acc*) or peduncle field (*pcc*) by extensions of the ventral field, forming small detached dark patches.

WHITE FIELDS/BLAZES. *Ventral field (vf).* This ivory white field covers the whole underside of the body, from the throat to the underside of the tail flukes (Figs 1B,1C). It is most extensive on the throat (except where it is partly infilled by

FIG 3 (facing). Dorsal and lateral colour elements. A, The dark grey spinal field (sf) extends along the back from the rostral saddle to the tail stock or peduncle; it is narrowest behind the dorsal fin where there is a dorsal extension of the posterior flank patch (pfp). The dark spinal field and posterior margin of the dark thorax field extend onto the anterior flank patch (afp) in a series of parallel dark "tiger stripes" (ts). The nape streak (ns) is thin throughout and extends down the right side to insert on the base of the flipper. B, The nape streak (ns) forms a diffuse patch (cf. the thin line shown in 2A). C, Diffuse extensions of the right and left thorax patches (thp) extend onto the back where they almost meet in an anteriorly directed peak, just to the left of the mid-line of the back. This takes the form of a nape streak but the actual nape streak (ns) can be seen in its usual position. The white arrow indicates the rostral saddle, with a strongly concave or scalloped trailing edge. Tiger stripes are clearly visible on the flank patch. D, The white ventral field extends upwards as a mandible blaze (mb) while the anterior half of the eyelids is white as an eye blaze (eb). The thin nape streak (ns) continues to the base of the flipper. The axillary patch (ap) is extensive and broadly attached to the thorax patch (see Fig. 4F for more detail). E, The posterior edge of the rostral saddle (white arrow) is straight. The nape streak (ns) bifurcates on the right side, with one branch directed posteriorly to join the anterior margin of the thorax patch, while the second branch continues to the base of the flipper. Note the broader, more anteriorly directed peak of the thorax patch (cf. D). The axillary patch is separate ("detached") from the thorax patch (cf. 3D). F, The right side of the rostral saddle (white arrow) extends further posteriorly and is more sharply defined than on the left side. The blowhole streaks (bs) are sharply defined, with the left blowhole streak curving to the left. The nape streak (ns) extends further onto the left side of the body.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the dark throat patch), the thorax and most of the abdomen. It narrows on the peduncle or tail stock where it is restricted to the ventral keel of the peduncle, before expanding to cover most of the flukes (Fig. 1C). The ventral field extends upwards onto the sides of the animal as (1) a mandible blaze (usually present on the right side of the body but only rarely on the left), (2) the shoulder blaze and (3) the peduncle blaze. The white of the ventral field may extend as splashes or streaks of white superimposed on the grey flank patch, which are particularly obvious when the flank patch is largely infilled by dark grey pigment.

*Mandible blaze (mb).* The whole of the left mandible margin is usually a dark grey colour, completely infilling the angle of the lower jaw (Figs 1B, 7A; Hoelzel & Stern, 2000: 23). On the right side, the white ventral field of the throat usually extends upwards on the angle of the lower jaw, sometimes almost on a level with the eye, as a mandible blaze. This colour asymmetry is particularly obvious on stranded animals, in which the muscles of the lower jaw have relaxed (Fig. 7B) showing much of the gape as lightly coloured. It is less obvious, but distinct, in living animals (Figs 2D, 3D,5A; Hoelzel & Stern, 2000: 26; Chadwick & Nicklin, 2001: 58-59, 66-67) in which the muscles adduct the lower jaw tightly against the rostrum (Lambertsen et al., 1995).

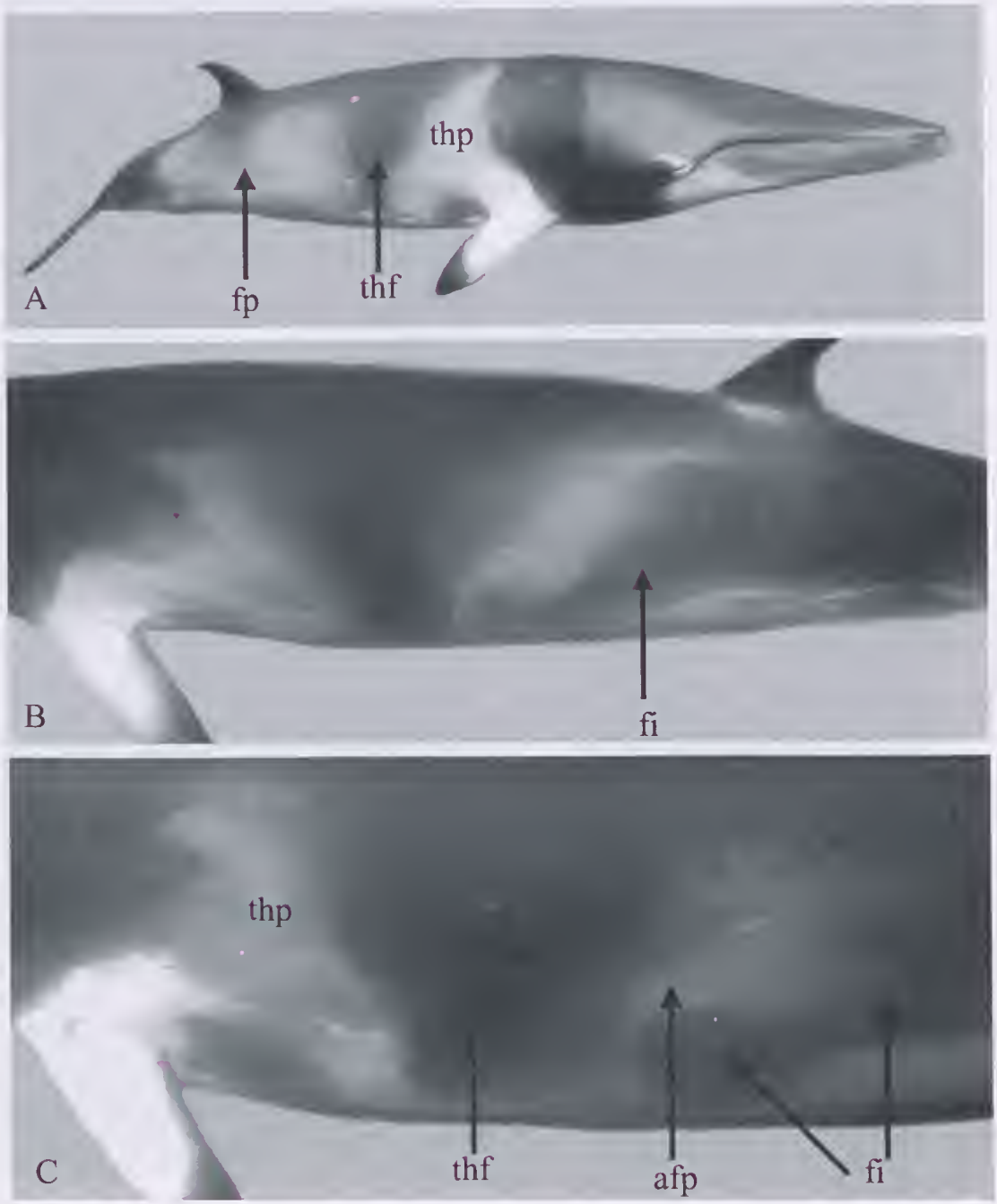
*Eye blaze (eb).* On the right side, white patches often occur over the anterior eye region and/or above the eye and may extend posteriorly to cover the entire region. Although most often covering just the anterior eye region (Figs 2D,3E, 5A), at its most extensive the white can cover most of both eyelids (palpebrae) as well as the dorsal and ventral folds (Figs 2D,3E; Hoelzel & Stern, 2000: 26 (nearer whale)). The eye blaze is usually absent from the left side of the body (compare right and left sides of whale in Fig. 7) but in those rare animals where an eye blaze is present on the left, the extent is reduced compared with its right eye blaze which is usually particularly well developed.

*Shoulder blaze (shb).* The shoulder blaze is bright ivory white; it occurs above the insertion of the flipper (Figs 1-7). The shoulder blaze is visible in all underwater photographs, even those in which the animal is distant (Fig. 1B; Laboute & Magnier, 1979: 136; Martin, 1990: 78 lower left). However, it often flares out because of the contrast with the predominantly grey animal. In photographs of stranded animals (e.g. Baker, 1983; Best, 1985), however, it may not always be possible to clearly separate the white shoulder blaze from the grey thorax patch above it. The shoulder blaze may merge posteriorly with an antero-dorsal extension of the ventral field so that the entire thorax patch is edged ventrally with bright white (Figs 1B, 3B, 3E, 4A,4C), however more usually the posterior margin of the shoulder blaze is defined by a variably developed dark axillary patch (see below).

*Peduncle blaze (pb).* The vertical components of the posterior and anterior caudal chevrons define

FIG. 4 (facing). Lateral thoracic colour elements. A, The ventral margin of the dark thorax field (thf) is broad and truncate. The posterior margin of the thorax field extends onto the light grey flank patch as a series of parallel dark thin "tiger stripes". The axillary patch is small, just behind the flipper. It is clearly separated from the thorax patch by white of the shoulder blaze and an extension of the ventral field. The dark distal flipper patch continues as a thin band along the trailing edge of the flipper, joining with the anterior extension of the axillary patch. B, The axillary patch is broadly attached to the thorax patch, dividing the white shoulder blaze from the extension of the ventral field. The axillary patch is "stacked", with layers of dark pigment one above the other. The ventral part of the axillary patch extends forward to the axilla of the flipper. C, The anterior margin of the thorax patch is sharply indented, with a prominent anteriorly directed peak. The white shoulder blaze is extensive, with only a small dark axillary patch seen just behind the flipper. Thus the axillary patch is broadly detached, as in A. The arrow indicates a light grey shoulder which extends from the posterior margin of the nape field onto the base of the flipper (same individual as in Fig. 3B). D, The axillary patch is broadly attached to the thorax patch and is more loosely stacked, with the individual layers of the axillary patch more clearly separated. The thorax patch is broadly truncate dorsally, with an ill defined anteriorly directed peak. E, The axillary patch (ap) is lightly attached by thin light grey streaks from the thorax patch, which separate the shoulder blaze (anteriorly) from an extension of the ventral field (posteriorly). The arrow indicates a light grey border from the distal flipper patch, extending onto the white of the basal flipper blaze. The ventral margin of thorax field is hooked forward towards the axillary patch. F, The axillary patch is broadly attached (cf. the broadly detached axillary patch in 4A and 4C, which is very clearly separated from the thorax patch by the white shoulder blaze and a dorsal extension of the ventral field). The axillary patch extends forward to the axilla of the flipper where it links with the thin dark grey pigment along the trailing edge of the flipper. The peak of the thorax patch is narrow and directed antero-dorsally (same individual as in Fig. 3D).

an area of white on the ventral field which extends upward into the dark peduncle field as a peduncle blaze (Figs 1A, 1C; Arnold et al., 1987, fig. 3c). The peduncle blaze can be vertical, directly above and at almost right angles to the chevrons (Fig. 1A, 1C), or angled forward to varying degrees. It usually forms a well defined streak up the side of the peduncle (see Figs above), but more rarely may be more diffuse, expanding dorsally as a light grey patch.



SADDLES, PATCHES & STREAKS. *Rostral saddle (rs).*The whole rostrum, back to the level of the reduced blowhole guard, is a lighter grey colour, which contrasts distinctly with the dark nape region (Figs 1A,2A,2B,3F,5A,6B). The rostral saddle usually is divided into a distinct right and left field by a medial forward extension of the spinal field reaching to the level of the blowholes (Fig. 3F). The right field generally extends further posteriorly along the back than does the left (Figs 2A, 2C,3F,6B). A forward extension of the dark nape field often creates a sharply defined, distinctly scalloped or concave posterior margin of the rostral saddle on the right side (Figs 2B, 6B; Clapham, 1997: 60; Chadwick & Nicklin, 2001: 61); other variations include a more convex (Fig. 3F) or straight (Figs 2D,5A) margin. The posterior margin of the left rostral saddle is usually much more diffuse, blending into the nape field (Fig. 3B).

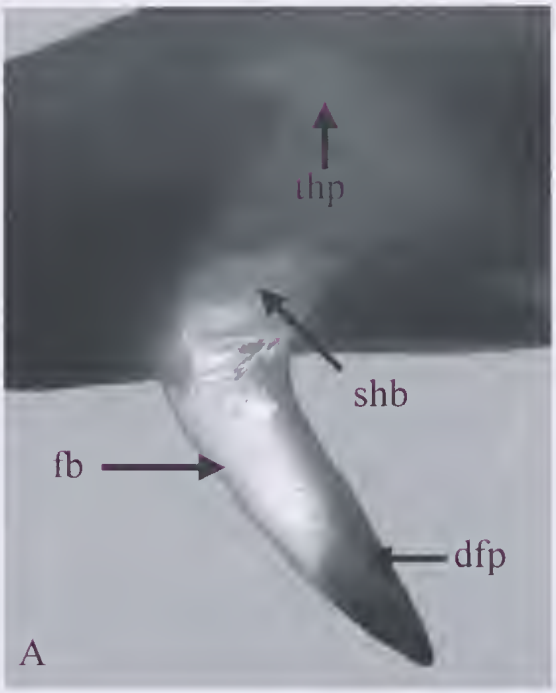
*Blowhole streaks (bs).* These light grey, thin lines originate from the posterior end of each blowhole slit. The right blowhole streak closely follows the medial margin of the right rostral saddle. It may run distinctly posteriad (Fig. 3F), but more frequently curves slightly to the left distally (Fig. 2C); in one animal seen in 2005 it diverged to the right. The left blowhole streak consistently and more strongly curves to the left (Figs 2A, 2C,3F,6B; Hoelzel & Stern, 2000: 14), generally running parallel to the convex posterior margin of the left rostral saddle (Fig. 3F; Clapham, 1997: 60; Chadwick & Nicklin, 2001: 61). We have seen no cases in which the left blowhole streaks ran to the right side of the body.

*Nape streak (ns).* Dorsally, the nape streak is usually a transverse thin light grey line against the darker background of the spinal field. It is always continuous across the back but is highly variable in form. The blaze can extend forward as a sharp peak on the midline of the body (Fig. 3A), form a straight line across the back (Fig. 2E), bow backwards in the midline (Clapham, 1997: 60) or be asymmetrical, extending further forward on the left side of the back (Figs 2A, 3F; Chadwick & Nicklin, 2001: 61). The nape streak often forms a sharp, almost right angle bend before descending down the sides of the nape field (Fig. 2E; Cox, 1989: 65; Hoelzel & Stern, 2000: 14; Chadwick & Nicklin, 2001: 58-59, 61). The individual shown in Chadwick & Nicklin (2001: 61) illustrates the sharp backward bend of the nape streak on either side of the back, however the pattern is somewhat obscured because the whole nape streak is shifted obliquely forwards and to the left, as is also the case in the whales shown in our Figs 2A & 3F. The dorsal portion of the nape streak may be sinuous (Fig. 2C), forming a complex pattern of grey on the spinal field and upper nape field.

Laterally, the nape streak continues down either side as a thin line (Figs 2A, 3A) or expands into a broad, diffuse grey patch which may be extensive (Figs 3B, 4C). The nape streak may angle sharply backwards about half way down the nape field and insert on the anterior margin of the thorax patch (Hoelzel & Stern, 2000: 26), continue ventrally to insert on the shoulder blaze just in front of the flipper insertion (Figs 2A, 2D,3A; Hoelzel & Stern, 2000: 6; Chadwick & Nicklin, 2001: 58-59) or bifurcate and insert on both these locations (Fig. 3E). The exact form of the nape streak is so variable that it can be used to recognise individual whales. However, the details are visible only on good video or photographs; indeed, the whole nape streak was missed by Arnold et al. (1987) in an earlier description of dwarf minke whales.

*Ear stripe (es).* This occurs only occasionally in dwarf minke whales. There is a fine line within

FIG 5 (facing). Flank colour elements. A, The thin cape-like thorax field (thf) divides the lateral light grey pigment into an anterior thorax patch (thp) and an extensive flank patch (fp), which is undivided by a flank infill. Also evident are the mandible blaze, eye blaze, a right rostral saddle with straight posterior margin, a thin nape streak which continues to the base of the flipper and a vertical white pigment band between the flank patch and dark peduncle field, which is a continuation of the peduncle blaze. This individual is unusually light in colouration, with an extensive rostral saddle, broad thorax patch and well developed flank patch. Two oval scars occur near the posterior edge of the thorax field; a parasitic copepod (*Pennella* sp.) trails from the lower oval scar. B, The thorax field is extensive in this individual and a well developed flank infill (fi) covers most of the flank region, leaving only a narrow light anterior flank patch. The flank infill continues forward and curves upward as a swirl or wave. The small axillary patch is broadly detached from the thorax patch. C, Another individual with a broad thorax field (thf), which is truncate ventrally; a small anterior flank patch (afp) is bounded by the thorax field anteriorly and an extension of the flank infill (fi) posteriorly. The flank infill expands anteriorly as a knob-like dark pigment patch. Tiger stripes extend into the anterior flank patch. The axillary patch is lightly attached.


thp
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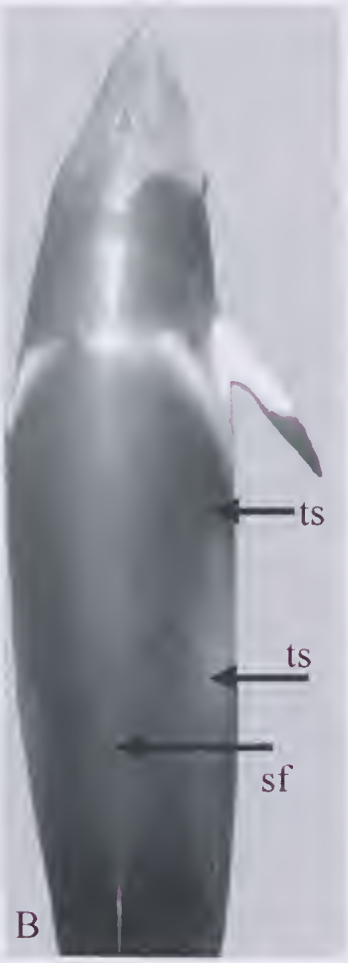
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the nape field, apparently an ear stripe, in photographs of a dwarf minke whale stranded on Pukehina Beach, Bay of Plenty, New Zealand (unpubl. photo, S. Gibney) and we have seen it on a number of individuals from northeastern Australia.

*Thorax patch (thp).* This light grey patch is usually triangular, with its base defined by the white shoulder blaze and antero-dorsal extension of the ventral field (Fig. 4C), and/or a variably developed axillary patch (see below). The anterior margin of the thorax patch is defined by the dark nape field. This anterior margin is sharply defined, and may be broadly concave (Fig. 4D) or sharply angled (Figs 4B, 4E), with an anteriorly directed peak (Fig. 4B). The dorsal border of the peak can be smoothly curved (Fig. 4E) or more flat and truncated (Fig. 4D; also compare animals shown in Chadwick & Nicklin, 2001: 66-67). The peak of the thorax patch generally extends higher on the right side of the body (Figs 5A, 7B) and may even extend across the midline of the back. The peak on the left side is usually lower and directed more anteriorly (Fig. 7A) but, rarely (Fig. 6B), may also extend medially so that right and left thorax patches almost meet on the back. The posterior margin of the thorax patch is defined by the thorax field; this edge may be diffuse, expanding as an indistinct cloud-like patch towards the midline (Figs 2A, 4B; Hoelzel & Stern, 2000: 14, 23 (same animal from different angles); Chadwick & Nicklin, 2001: 58-59).

*Axillary patch (ap).* Arnold et al. (1987) described a dark patch within the shoulder blaze which was completely surrounded by white; they called this the 'flipper oval' (Arnold et al., 1987, fig. 1). Subsequent field observations show that this 'flipper oval' is just one variation in the general shoulder region pigmentation. A dark patch is always present, though sometimes reduced in size (Fig. 4C). It may be completely separated dorsally from the thorax patch ('detached') and thus is completely surrounded by the white of the shoulder blaze merging with an extension of the ventral field (Fig. 4C; Cox, 1989: 65; Hoelzel & Stern, 2000: 14, 23 (same animal)); narrowly attached to the thorax patch (Figs 4E, 5C; Arnold et al., 1987, fig. 3e) or broadly attached to the thorax patch (Figs 1A, 2D, 3D, 4B, 4F, 6A; Chadwick & Nicklin, 2001: 58-59, 66-67). In the last case, the dark patch largely infills the extension of the white ventral field so that the only major area of white is the shoulder blaze above the insertion of the flipper (Fig. 6A). A broadly attached axillary patch looks like an extension of the thorax patch (Figs 1A, 4F). The patch may be entire and broadly rounded (Fig. 5C) or may be more acute anteriorly and posteriorly, so that the patch appears to be broadly bifurcated (Fig. 4B). In other cases, the margins of the dark patch may be deeply serrate, appearing as a vertically "stacked" series of dark bands (Fig. 4B). In some animals these may be reduced so that they are separated from each other or even so reduced as to form one or two small oval blotches one above the other in the ventral field (Fig. 4D).

The dark patch (or at least one of the patches in the rarer cases when there is more than one patch on the ventral field) runs forward to the axilla of the flipper and is generally continuous with the dark pigment running along the trailing edge of the flipper (Figs 3D, 3E, 4B, 4D-F; Best, 1985, fig 1e; Hoelzel & Stern, 2000: 14, 23). This can be clearly seen when the flipper is held out and downwards from the body (Fig. 4) but may not be visible in photographs of stranded animals, where the flipper is held closer to the body. Given its consistent occurrence at the axilla of the flipper, we suggest that a more general term for the dark patch in the shoulder blaze is 'axillary patch', which we propose should replace the term 'flipper oval'.

*Flank patch (fp) and flank infill (fi).* The generally light grey flank patch extends from the

FIG 6 (facing). Colour variations. A, An extensive axillary patch, broadly attached to the thorax patch (thp) reduces the extent of the shoulder blaze (shb) to an area just above the flipper base. The dark distal flipper patch (dfp) extends along the trailing edge of the flipper in a particularly broad band (cf. individuals shown in Fig. 4A-F) which extends forward into the white flipper blaze (fb) at the base of the flipper. A light grey shoulder extends from the nape field backwards onto the flipper blaze at the base of the flipper. This individual shows particularly extensive infilling of the flipper blaze. B, The dark spinal field (sf) is narrowest just before the dorsal fin due to a dorsal expansion of the flank patch. Well developed tiger stripes (ts) extend from the spinal field and posterior edge of the thorax field onto the flank patch (same individual as in Fig. 3C). C, Dark flecks or mottling (m) of the back may be pigment or due to flaking of the skin. This individual has a broadly attached, extensive axillary patch, reducing the extent of the shoulder blaze. D, Close-up of individual shown in Fig 1B, showing the streaks and speckling (s) from the dark flank patch on to the white ventral field.

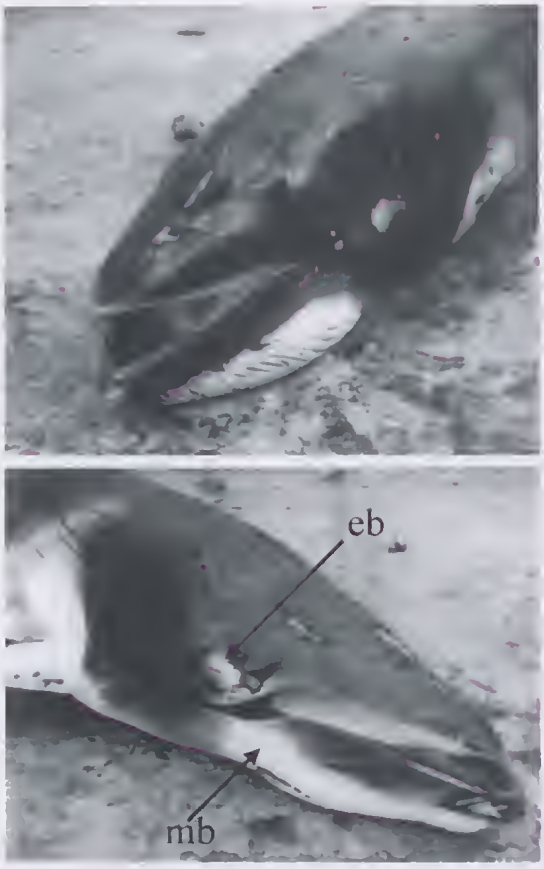


FIG. 7. Dwarf minke whale stranded at Lady Elliot Island, showing characteristic asymmetry. There is a mandible blaze (mb) and eye blaze (eb) on the right side but the mandible is completely dark on the left side, with no eye blaze (the white behind the eye is an abrasion). The dark border of the left mandible is continuous with the dark throat patch, making the left side appear distinctly darker than the right side of the head and shoulder region. The thorax patch extends high up the right side, while it is lower and angled more strongly forward on the left side. There is a less obvious demarcation of the white shoulder blaze and light grey thorax patch than in photographs of living dwarf minke whales.

dark thorax field to the peduncle field. It is bordered ventrally by the white ventral field and can be almost entirely light grey (Fig. 5A), or variably obscured by the flank infill, which can vary considerably in size and shape. The most frequent infill is the anterior triangle (Fig. 1A). The apex of the triangle may form a broad, dorsally directed swirl (Paterson, 1994, fig 2, lower; Secchi et al., 2003, fig 1) or a more elongate, thin swirl with the fine tip, curled like a Salvador Dali moustache (Figs 1C, 5B). The curled tip may itself be infilled, creating a knob at the end of the swirl (Fig. 5C). Where infilling occurs, the flank patch is divided into an anterior flank patch and posterior flank patch (Fig. 1A: *afp, pfp*). Cox (1989: 65) illustrated major infilling, with only a small anterior flank patch in front of the dorsal fin; similarly extensive infilling is shown in Fig. 5B, C. The most extensive infilling obscures most of the flank patch so the ventral field is edged with darker grey, which make any dorsal splashes or swirls from the white ventral field or speckling and streaking (Figs 1B, 6D) stand out.

*Tiger stripes (ts).* These parallel, dark, usually vertical stripes extend from the spinal field and thorax field onto the flank patch. They may occur on the anterior margin of the thorax field in which case they extend downwards onto the thorax patch (Figs 3C, 5C, 6B) or they may extend from the ventral margin of the thorax field onto the white ventral field.

*Speckling (s).* Speckling or streaking can occur particularly along the lower edge of the flank patch or on the adjacent margin of the ventral field (Figs 1B, 6D). This can be grey pigment against the white of the ventral field or white pigment on the grey of the flank patch.

*Mottling (m).* The dark grey of the spinal field, upper nape field and thorax field, as well as the dorsal fin and upper sides of the flukes, may contain patches of light grey mottling of variable size and shape (Fig. 6C). These light patches do not appear to be distinct colour elements but may reflect a condition of the skin (e.g. patches which are about to be, or have recently been, sloughed).

FLIPPER. *Flipper blaze (fb).* The base of the flipper is consistently filled by a white blaze (Figs 1-7). The white is most extensive on the anterior half of the flipper, occupying about two thirds of the flipper length as seen from above, with the white continuing along most of the leading edge of the flipper.

The insertion of the flipper is predominantly white (Figs 1A, 2A, 3D, 3E, 4B-F). There are individual variations in the amount of speckling and/or dark patches over the white flipper blaze (compare Figs 2A & 2B). Usually the light grey of the thorax patch extends ventrally along the posterior margin of the nape field and onto the base of the flipper, forming a light grey shoulder of variable size and shape (Figs 2B, 4C). Rarely (Fig. 6A; Kato & Fujise, unpubl. data) this light

Table. 1. Coding for phylogenetic analysis. Numbers in bold in the first row indicate the characters used (1: rostral saddle, 2: blowhole streaks, 3: dark nape field, 4: form of dorsal portion of nape streak, 5: ventral nape streak, 6:ear stripe, 7: basal flipper colouration, 8: distal flipper colouration, 9: axillary patch, 10: thorax field, 11: caudal chevron, 12: peduncle streak, 13: asymmetry). See Appendix for basis of character coding.

| | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** | **9** | **10** | **11** | **12** | **13** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Physeter* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Balaena* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Eubalaena* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Caperea* | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Eschrichtius* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Megaptera* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *B. musculus* | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| *B. physalus* | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | 2 |
| *B. borealis* | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 0 | 1 |
| *B. bonaerensis* | 0 | 2 | 1 | 1 | 1 | 1 | 3 | 1 | 1 | 3 | 2 | 1 | 1 |
| Dwarf minke | 2 | 1 | 1 | 2 | 0 | 1 | 2 | 2 | 2 | 3 | 2 | 2 | 1 |
| *B. acutorostrata* | 1 | 1 | 1 | 2 | 0 | 1 | 3 | 2 | 1 | 3 | 2 | 2 | 1 |

grey shoulder of the thorax patch extends posteriorly towards the axillary pigment, which together may create an interrupted thin grey strip across almost the entire width at the base of the flipper. The dark nape field may also extend onto the base of the flipper; at certain angles this suggests that at least part of the base of the flipper is dark (Fig. 2A). However, none of the infillings of the flipper base approaches the dark base in the common minke whale or the type 2 flippers of the Antarctic minke whale (Appendix).

*Distal flipper patch (dfp).* The distal part of the flipper is covered by a dark grey patch (Figs 1-7), edged proximally with a light grey border (Fig. 4E). There are individual variations in the extension of this light grey border of the dark flipper patch, often forming streaks or patches extending onto the white flipper blaze (Figs 2B, 3E, 4E, 6A).

The proximal margin of the dark flipper tip runs obliquely backwards so that the entire rear margin of the flipper to the axilla has a dark grey edge (Figs 3E,4D,4F; Chadwick & Nicklin, 2001: 58-59). This dark margin is generally continuous with the axillary patch. The dark flipper patch can be seen on the underside of the flipper (Fig. 1C), which also mirrors the more extensive distribution of white along the anterior half of the flipper.

The overall colour pattern of the flipper is remarkably consistent in the >200 different individuals on which this paper is based, and in the photographs of animals from South Africa, New Zealand, New Caledonia and Brazil (Baker, 1983; Best, 1985; Cox, 1989: 65; Laboute & Magnier, 1979; Martin, 1990: 78; Zerbini et al., 1996; Secchi et al., 2003).

## PHYLOGENETIC ANALYSIS

The colour coding is given in Table 1. Given that the Antarctic minke whale exhibits two pigment types, type 1 (monotone) flipper and type 2 (two-tone) flipper, two analyses were done with basal flipper colour coded 1 and 3 respectively. In the first analysis, an exhaustive search returned a single tree (Fig. 8) with a consistency index of 0.839 and a rescaled consistency index of 0.743. With the flipper base coded 3, the same tree was recovered, with a consistency index of 0.839 and rescaled consistency index of 0.886. The transformation series given below refers to the first analysis only.

The common and dwarf minke whales were united by the following characters: dorsal and lateral nape streak linear or diffuse (not V-shaped), ventral nape streak (Appendix, section 5) absent, distal flipper patch present (and white flipper blaze variably developed), and peduncle blaze well developed. The last character may not be consistent as the peduncle blaze and white up the side was clearly visible in only one photograph of a common minke whale (Norris & Prescott, 1961 (Appendix, section 12)). However the other characters represent well defined and consistent (hence diagnostic) synapomorphies in the nape streak and flipper, separating both common and dwarf minke whales from the Antarctic minke whale.

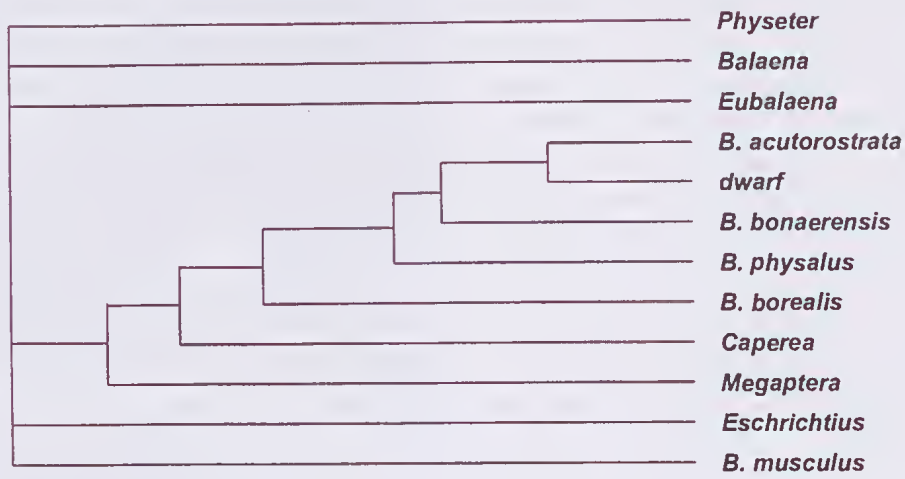


FIG. 8. Cladogram based on 13 colour elements (see Table 1 and Appendix for details).

The common, dwarf and Antarctic minkes were united based on a double caudal chevron, a peduncle blaze in the ventral field, and a cape-like dark thorax field, separating the grey of the sides into a distinct anterior thorax and posterior flank patch. The peduncle blaze is partially a correlate of the double chevron, which defines an area of white separate from the rest of the ventral field of the caudal peduncle. However, the double caudal chevrons and thorax field represent well supported and consistent synapomorphies of all the minke whales.

The minke whales and fin whale were united based on at least one caudal chevron (one in fin, two in the minkes); a ventral nape streak (shared only by fin and Antarctic minke whale) and uniform coloured flipper base and tip, with white leading edge (shared only by fin and Antarctic minke whale). This grouping was poorly supported with reversals of colour characters in the dwarf and common minke whales.

The minkes, fin and sei whales were united as a general *Balaenoptera* clade, united by colour asymmetry (though this is strongly developed only in the fin whale and at least some individuals of Bryde's whales and *B. omurai*), grey along the sides of the body (versus uniform or black and white colour of more basal taxa), blowhole streaks, ear stripe and possibly axillary patch (best defined in minke whales, and especially dwarf minke whale). Table 2 shows the distribution of colour elements in *Balaenoptera* species. *B. omurai* is not included because its colour pattern is insufficiently known. The taxonomy of the Bryde's whale complex is unresolved, therefore colour elements documented in the literature may refer to more than one species. Thus "Bryde's whales" were excluded from the cladistic analysis, however some information on one population is included in the Table based on underwater video (BBC: *Wild Australasia: Southern seas* and by Peter Constable) of individuals taken at Turtle Bay, Dirk Hartog Island, Western Australia (see Appendix for more details). Table 2 indicates that blowhole streaks and an ear stripe occur in at least some individuals of fin, sei, Bryde's, common, dwarf and Antarctic minke whales, though they may be too inconsistent to be diagnostic. The light grey lateral field occurs in all but the sei whale. A light grey flipper, with light grey to white leading edge, occurs in all *Balaenoptera* species except the sei, common and dwarf minke whales (though the white of the flipper blaze is most extensive anteriorly in the last two species). Colour asymmetry (with the right side lighter) is variably developed but has been reported in at least some individuals of fin, sei, Bryde's, Antarctic and dwarf minke whales, as well as *B. omurai*. The common minke whale may also be asymmetrical (the rostral saddle appears to be better developed on the right side of an individual illustrated in Hoelzel & Stern, 2000) but there is

Table 2. Colour characters of mysticete whales. The colour characters for Bryde's whales are based on video of whales from Western Australia and relate only to that population. Question marks indicate that there is no information in the literature or that the evidence is especially equivocal. In the last row (Asymmetry), 'C" indicates that there is consistent asymmetry, + indicates that asymmetry has been documented in at least some individuals and ?, as above, indicates that information is unavailable or equivocal for the taxon (or, in the case of "Bryde's whale", Western Australian population) used for coding. Abbreviations include bowh=bowhead, humpb=humpback, Brydes (WA)= Western Australian population of Brydes whale species complex, omurai= *Balaenoptera omurai*, Antarc= Antarctic.

| | sperm | right | bowh | pygmy right | gray | humpb | blue | finback | sei | Brydes(WA) | omurai | common minke | dwarf minke | Antarcminke |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Rostral saddle | | | | + | | | | + | + | | + | + | + | |
| Nape streak | | | | + | | | | + | | + | ? | + | + | + |
| Blowh Steak | | | | | | | | + | + | + | ? | + | + | + |
| Ear stripe | | | | | | | | + | + | + | ? | + | + | + |
| Lateral field | | | | + | | | | + | | + | ? | + | + | + |
| Light distal,white leading edge | | | | | | | + | + | | + | + | | | + |
| Asymm | | | | | | | ? | +C | + | ? | + | ? | +C | + |

insuffieient information in the literature to determine asymmetry/ symmetry of eolour in that taxon.

The "*Balaenoptera*" elade and *Caperea* were united based on a rostral saddle, defining a dorsal nape field, plus a V-shaped dorsal nape streak.

*Megaptera* was united with *Balaenoptera* and *Caperea* based on a blaek or dark grey and white eolour pattern (as opposed to the uniform eolouration of more basal taxa).

The blue whale was separated from the other balaenopterids, while *Eubalaena, Balaena* and *Eschrichtius* showed no variation from the outgroup *Physeter*.

## DISCUSSION

COLOUR PATTERN VARIATIONS. Best (1985), based primarily on speeimens from South Afriea, documented a 'diminutive form' of minke whale with an unusually large proportion (relative to Antaretie minke whales) of light baleen plates, a white flipper base (our "flipper blaze") eonfluent with a white shoulder pateh (our "shoulder blaze") and dark pigment in the neek region extending onto the ventral grooves (our "dark throat pateh"). He was able to identify one or more of these features in speeimens from Australia, New Zealand and Brazil. Arnold et al. (1987) eonfirmed all these features in 14 speeimens from eastern Australia and extended the detail of the eolour pattern deseription. They noted the elear separation in eolour patterns between the dwarf and 'ordinary' form (now reeognised as *B. bonaerensis*) and argued that they were taxonomieally distinet. However at that stage material was insuffieient for a formal deeision.

The present paper greatly extends the sample size (>200) for Australian waters and ineorporates new information from New Zealand, Vanuatu, Fiji and Brazil. It eonfirms that the eolour patterns identified by Best eo-oeeur eonsistently over the whole southern hemisphere range of dwarf minke whales. There may be eonsiderable variation in the development of the axillary pateh of dwarf minke whales and a eorresponding ehange in the extent of the shoulder pateh. Infilling of the flank pateh is also variable and can produee eonsiderable differenees in the darkness of individual whales. None of this variation ehanges the faet that the eolour elements reeognised by Best (1985) and Arnold et al. (1987) are eonsistent.

The elear separation in the eolour patterns of dwarf and Antaretie minke whales is also maintained with the larger sample size, with no evidenee of intermediate eolour patterns between

the two taxa. Off South Africa, there is evidence that dwarf and Antarctic minke whales occur in different habitats, with the dwarf minke whale occurring in more coastal waters (Best, 1985). The separation is not absolute, however. Kasamatsu (1988) documented dwarf minke whales several hundred kilometres off the Western Australian coast in oceanic waters. On July 6, 2000, at Reef 15-040 (15°23.15'S. 145° 45.78'E), we were in contact with four dwarf minke whales which were briefly joined by an immature Antarctic minke whale. Such instances, however, are still exceptional, and there may sufficient ecological separation of dwarf and Antarctic minke whales to maintain a partial reproductive barrier. Intraspecific geographical variation, including distinctive colour patterns, is well documented in delphinid cetaceans, e.g. Commerson dolphin, with a distinctive disjunct population around the Kerguelen Islands (Pichler et al., 2001), Hector's dolphin with a subspecies restricted to the North Island of New Zealand (Baker et al., 2002), the 'truei' variant of Dalls porpoise (Amano & Miyazaki, 1996) and pilot whales off Japan (Kasuya et al., 1988). However, the consistent occurrence of the colour elements throughout the extensive range of the dwarf minke whale and the lack of intermediate colour patterns linking it with the Antarctic minke whale, despite their overlaps in occurrence throughout their ranges, contrast with the regional differences in colour patterns of the delphinids just quoted. This indicates that the dwarf minke whale and Antarctic minke whales are reproductively isolated and thus supports their status as distinct species. The colour features are sufficiently consistent to allow separation of dwarf and Antarctic minke whales in the field, at least if they are seen under favourable conditions.

PHYLOGENETIC ANALYSIS. Whereas the colour pattern data can be used as evidence of reproductive isolation between the sympatric to parapatric populations of dwarf and Antarctic minke whales, taxonomic inferences are more difficult in the case of the allopatric populations of dwarf minke whale and the common minke whale.

Using a combination of osteological, limited morphometric and colour pattern data, Arnold et al. (1987) suggested that the dwarf minke whale was more closely related to the common (northern hemisphere) minke whales than to the 'dark shoulder' or 'Antarctic minke' (*B. bonaerensis*), a view already anticipated by Best (1985). This was based on a limited sample size but, more importantly, was essentially phenetic without an indication of possible phylogenetic features.

The diagnostic features of the dwarf minke whale (dark throat patch, shoulder blaze, white flipper blaze) are autapomorphies and thus of no phylogenetic significance. In this paper, we present a cladistic analysis based on 13 other colour elements which show a greater potential to establish taxonomic relationships. It must be noted that the resulting cladogram poorly reflected the presently recognised families of baleen whales and contained no monophyletic groups. Nonetheless, the analysis did suggest several taxonomic relationships.

In our analysis, the common and dwarf minke whales were united based on their more specialised flipper colouration (diverging from the more general pattern of a uniform dorsal pigment with a light grey to white leading edge as found in Antarctic minke whales), more specialised nape streak (linear to diffuse, in contrast to the more generalised V-shaped dorsal streak found in balaenopterids including the Antarctic minke whale), and the lack of a ventral nape streak element which creates the W-shaped chevron found in fin and Antarctic minke whales. The presence of these synapomorphies in colour elements provides evidence that the dwarf and common minke whales are sister taxa, sharing a more recent ancestry than either does with the Antarctic minke whale. This phylogenetic pattern is consistent with previous studies based on morphology (Best, 1985; Arnold et al., 1987; Zerbini et al., 1997) and molecular data (Wada & Numachi, 1979; Pastene et al., 1994).

All minke whales shared a set of specialised colour characters, primary of which is the separation of the lateral light grey field by a dark cape-like thorax field into an anterior thorax patch and a posterior flank patch, as well as the development of a double caudal chevron.

Finally there was a suggestion of a suite of colour elements which may be characteristic of most *Balaenoptera* species (Table 2). These include variably developed left-right colour asymmetry, blowhole streaks, ear stripe and generalised light grey pigment area along the sides of the body between the darker grey spinal field and white ventral field. It is often stated that the fin whale is the only consistently asymmetrical species. However a consistent,

albeit more subtle, left-right asymmetry occurs in dwarf minke whales. Strikingly asymmetric individuals within the Bryde's whale species complex and *B. omurai* have also been documented (see Appendix, section 13). The uniformity of colour elements among sei, fin and all the minke whales provides no support for the separation of minke whales from other rorquals as suggested by Árnason & Gullberg (1994), based on cytochrome b gene sequences. However, except for possible asymmetry of colour and generalised flipper pigment in blue whales (Appendix), neither the blue whale nor the humpback whale show any of these colour elements. Such differences in colour have previously been attributed to differences in life style (either habitat and/or diet), e.g. the uniformly mottled colour of the blue whale has been linked to its obligate planktivory. However, this does not explain the lack of certain colour elements such as the V-shaped dorsal nape streak which is not present even in foetal blue whales (Mackintosh & Wheeler, 1929), in marked contrast to fin and sei whales (Mackintosh & Wheeler, 1929; Matthews, 1938) in which the streak is even more distinct in foetal whales than in the adult. Fossil evidence (Fordyce & deMuizon, 2001) indicates that the humpback whale diverged early from the other balaenopterids (Miocene, 11-12 million years ago) and it already has been placed in a separate genus (and even subfamily) based on morphological differences in the size of flipper and form of scapula. The lack of any of these "*Balaenoptera* colour elements" in the blue whale suggest that it may also represent a lineage which diverged early within the evolution of *Balaenoptera*. However, the relationships within balaenopterid whales remain unresolved, including a recent molecular study (Rychel et al., 2004) which presented a range of different phylogenies depending on the molecular marker and type of analysis used.

At the highest levels, the phylogenetic signals within colour patterns appear weak. *Caperea*, which is generally placed in its own family, Neobalaenidae (Miller, 1923; Barnes & McLeod, 1984; Árnason & Gullberg, 1994) based on morphological and molecular data, was placed with the fin, sei and minke whales (all family Balaenopteridae), while other balaenopterids such as the humpback whale and blue whale were separated from this clade (Fig. 8). The more uniform colour patterns of the balaenids and gray whale (Eschrichtiidae) provided no evidence on the relationships of those taxa. Their similarity in colour elements to the outgroup, the sperm whale (as well as to many beaked whales), suggests that uniform colouration is the ancestral pattern for mysticetes.

TAXONOMIC IMPLICATIONS. Despite the lack of monophyletic groups, the phylogenetic analysis did provide support both for the close relationships of all minke whales, and particularly the common and dwarf minke whales. However it gives no indication of the taxonomic level at which the dwarf minke whale should be recognised (i.e. species or subspecies).

Within phylogenetic studies, any taxon which can be diagnosed is usually recognised as a species. However this merely represents a convention and it is hard to see how there can be an operational definition of a phylogenetic species when the technique depends on recognition of shared specialised features to establish common ancestry yet species themselves are diagnosed on the basis of autapomorphies which have no phylogenetic significance.

Even with molecular data, taxonomic differences are particularly difficult to infer when the compared populations are allopatric (Helbig et al., 2002; Milinkiviteh et al., 2001). If, as suggested by Helbig et al. (2002), it is practically impossible to directly test the ability to interbreed in allopatric populations (e.g. dwarf and common minke whales, which occur in different hemispheres) then one wonders whether there can be an operational species definition based on the biological species concept. The biological species concept is further compromised by data (Bérubé, 2002) which suggests that finback and blue whales (whose species integrity is well supported by both morphological and molecular data) can hybridise.

Molecular analysis of minke whales by Goto & Pastene (2000) grouped common minke whales from the North Atlantic and dwarf minke whales, both of which were distinct from all samples of common minke whale from the western North Pacific. However, an analysis presented by Baker et al. (2000) linked the western Pacific common minke whales in one cluster, common minke whales from the North Atlantic in another cluster and the dwarf minke whale in a third cluster, as an unresolved trichotomy. This could be considered evidence that the western North Pacific common, North Atlantic common and dwarf minke whales are all phylogenetic species (Baker et al., 2004),

clearly a different taxonomic hypothesis from that suggested by the data in Goto & Pastene (2000).

Mayr (1969) suggested that in doubtful cases of separation between allopatric populations, that the taxa be considered as subspecies. On this basis, we agree that the dwarf minke whale should be recognised as a subspecies of the common minke whale as suggested by Rice (1998), based on available information. We do not make any formal taxonomic decisions, as the status of the dwarf minke whale (as well as western North Pacific common minke whales, with an unresolved relationship to the nominal taxon *B. a. scammoni*, described from the eastern North Pacific) must eventually be decided based on the full range of characters and extent of concordance in osteological, morphological and molecular data from throughout the range of all the minke whale taxa. We do note, however, that there are consistent, diagnosable differences in the colour pattern of the dwarf minke whale which are more extensive than the colour pattern variations between the nominal subspecies of common minke whales (*B. a. acutorostrata, B. a. scammoni*) from the North Atlantic and North Pacific respectively. This suggests that the dwarf minke whale may warrant species rather than subspecies recognition.

ECOLOGICAL VERSUS PHYLOGENETIC BASIS FOR COLOUR PATTERN VARIATIONS. The possible influence of ecological factors should be noted. Brodie (1977) suggested the white flipper bands of northern hemisphere minke whales might be used in herding schooling fishes. Although the dwarf minke whale, also with white flippers, is known to feed on fishes (Kasamatsu et al., 1993), the 'herding hypothesis' does not explain the complex patterns of white, light grey and dark grey found in all minke whales.

Yablokov (1963, in Mitchell, 1970) contrasted three colour patterns: (1) uniform, which he associated with obligate planktivores or deep divers, (2) countershaded, which he linked to species feeding on nekton in the photic zone and (3) discretely bounded, which Yablokov linked to intraspecific signalling.

Minke whales in general, and dwarf minke whales in particular, have discrete pigment patches. There is evidence that common minkes of the north Atlantic, Antarctic and dwarf minke whales spend at least part of their life cycle in low latitudes where the water is clear (tens of metres) even in coastal areas and extremely clear (50-100m) in the open ocean. Dwarf minke whales are relatively small for a baleen whale so that the whole whale is clearly visible underwater and the colour elements – especially the white flipper base and shoulder blaze in dwarf minke whales – stand out right to the limits of underwater visibility (pers observations; also note photographs). In close contact (10-100m) visual signals have greater potential to identify individual whales than the vocalisations which are intense (Gedamke et al., 2001), essentially omnidirectional and thus difficult to localise. They could also be used in positioning and orienting to other whales collaborating in cooperative hunting manoeuvres. The complexity and strongly contrasting colour patterns in minke whales, especially the dwarf minke whale, is consistent with Yablokov's hypothesis and suggests that vision is an important sense when minke whales are close together.

Despite this behavioural 'overlay' there appears to be a phylogenetic basis for the variation in the colour elements, as indicated by the cladistic analysis. As in other groups of animals, the phylogenetically significant characters may not be the most obvious features of the whales and may be visible only in good photographs of living or very freshly stranded whales. For example, the blowhole streak was not recognised in any balaenopterid until 1985 when it was described in the Antarctic minke whale by Best (1985). It was initially missed in an earlier description of Australian dwarf minke whales (Arnold et al., 1987) and we also document it for the first time in the common minke whale in the present paper, based on photographs of live animals (e.g. Hoelzel & Stern, 2000).

Such photographs are particularly limited for sei whales and any of the Bryde's whale complex, but even in relatively "well known" species such as fin whales, the colour patterns are only poorly documented. Ironically, within the minke whale complex, it is in the common minke whale of the northern hemisphere that colour patterns are most poorly documented. We hope that by making others aware that balaenopterid whales have a range of consistent colour elements, that those with the opportunity to take photographs of living whales will record such features. It is only with a better range of photographs that we will be able to check whether our interpretation of the

literature is correct and thus test the validity of the taxonomic hypotheses suggested by our cladistic analysis.

The recognition that such features as colour asymmetry, V-shaped dorsal napestreak and rostral saddle may be more generally distributed within species of the genus *Balaenoptera* suggests that great caution is necessary in the identification of rorquals from field photographs, especially in the tropical Indo-Pacific with its complex of poorly known Bryde's whales. For instance, there seem to be greater similarities in the colour pattern of some Bryde's whales and the Antarctic minke whale than generally acknowledged in the literature (see, for example, photograph of a confirmed Bryde's whale in Baker, 1983). Resolution of these problems will require that good colour data, morphometrics, osteology and molecular data be available from the same specimens. The recent history of minke whale studies, in which clear taxonomic differences are being recognised in what was previously considered a single, highly variable species, suggest that similar studies on other balaenopterids will be equally useful, especially in establishing visual field characters.

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## APPENDIX

## CODING OF COLOUR CHARACTERS

*1.Rostral saddle.* The rostral saddle has not been doeumented in the Antaretie minke whale (Best, 1985; Bushuev & Ivashin, 1986). There is no indieation of a rostral saddle in blue whales (True, 1904), humpbaek whales, gray whales, right or bowhead whales, nor the outgroup, *Physeter.* All are thus eoded 0.

The rostral saddle was not doeumented in live *Caperea,* from South Afriea (Ross et al., 1975). However, Arnold (1987) and Matsuoka et al. (1996, fig 1) show a pygmy right whale *Caperea marginata* in whieh the head was distinetly lighter than the nape region, and it is thus eoded rostral saddle present (1)

The rostral saddle is eoded as present (1) in sei whales based on the photographs in Clapham (1997: 52,55). The latter pieture shows a dark eye stripe and light head (i.e. rostral saddle); this pattern was noted in 7% of sei whales examined in the Antaretie by Matthews (1938).

The rostral saddle is eoded present (1) in the eommon minke whale based on its oecurrenee at least in North Paeifie minke whales. The light head is obvious in Dorsey et al. (1990, fig. 7 (right sides of 7A, 7C, 7D, 7E, 7H; left side of 7E; Lien & Katona 1990: 33). The light head in more photographs of the right side may indieate that the rostral saddle is better developed on that side in north Paeifie minke whales, as is the ease with the dwarf minke whale. A surfaeing Northern Hemisphere minke whale shows a distinet right posterior extension of the rostral saddle with a sealloped posterior margin (Hoelzel & Stern, 2000: 39), as is seen in dwarf minke whales.

Although it is the asymmetrie nature of the eolour pattern whieh has been emphasized in fin whales *Balaenoptera physalus* (e.g. underwater photographs in Kiefner, 2002: 66,67) it is elear that the whole head ean be light eoloured, as a rostral saddle (e.g. aerial photos in Leatherwood et al., 1988, fig 26; Reeves & Mitehell, 1991, fig 11). On the right side, it is defined by the dark eye stripe, whieh is perhaps all that is left of a more extensive dark nape field; the details of the left nape field are unelear. At least on the right side, the rostral saddle is very well developed, thus it is eoded as 2. Similarly, based on data in this paper, the rostral saddle of the dwarf minke whale is eoded well developed (2).

*2. Blowhole streaks.* There is no evidenee for blowhole streaks in sperm, right, bowhead, pygmy right, gray, humpbaek or blue whales, despite the abundanee of detailed photos of live animals. All are seored 0 (blowhole streaks absent).

Minasian et al. (1989: 49) have a photograph of a northwest Atlantie fin whale with what appears to be a very elear left blowhole streak; the right blowhole streak is more obseure and appears to run just medially to the posterior extension of the right rostral saddle. A fin whale from the Gulf of California (Readers Digest, 1997) shows what appears to be a distinet left blowhole streak although it is partially obseured by dappling of the water surfaee. Blowhole streaks are visible in underwater video of a fin whale in the BBC doeumentary *Blue Planet (Tidal seas* episode).

Blowhole streaks are not visible in underwater photographs of sei whales in Williamson (1972) but the whole dorsal surfaee of the whales was heavily dappled from surfaee light refraetion. The photograph of a sei whale (Clapham, 1997: 52), shows what appear to be blowhole streaks in the same general position as in the dwarf minke and fin whales. Images of Bryde's whales from Western Australia feeding on bait balls (BBC doeumentary series *Wild Australasia: Southern seas)* show what appears to be blowhole streaks.

Blowhole streaks oeeur in at least some North Paeifie minke whales (Norris & Preseott, 1961, pl. 40b; Hoelzel & Stern, 2000: 39). They appear similar to the blowhole streaks of dwarf minke whales, as doeumented in this paper. Turner (1891-92: 49), deseribing a minke whale from Seotland, noted that 'a thin grayish band passed for several inehes horizontally behind the blowholes'- a good deseription of blowhole streaks.

Based on these literature reeords for finback, sei and eommon minke whales, and this paper for dwarf minke whales, all are seored as 1 (blowhole streaks present). Best (1985) first doeumented blowhole streaks, in the Antaretie minke whale. They seem to be better developed in that speeies than in the dwarf minke whale (Best, 1985) or in the northern hemisphere minke whales. The Antaretie minke whale is thus eoded 2 (blowhole streaks well developed).

*3. Dark nape field.* Sperm, right, bowhead, gray and humpbaek whales have a uniform dorsal eolouration and there is no elearly defined nape streak in photographs of any of those speeies. They are thus eoded 0 (dark nape field absent).

The nape area appears dark, eontrasting with a light rostral saddle in pygmy right (Matsuoka et

al., 1996), fin (True, 1904; Kiefner, 2002) and sei whale (Clapham, 1997). There are varying degrees of light grey just above the flipper in fin whales, containing light streaks diverging forwards and posteriorly from the flipper (True, 1904). In fin and sei whales, the darkest area of the nape may be restrieted on the right side to a dark band running dorsally and backwards from the eye. Nevertheless there is a dark nape area and pygmy right, fin and sei whales are all eoded as 1 (dark nape field present).

The dark nape region is obvious in photographs of northern hemisphere minke whales (e.g. Norris & Preseott, 1961, pl. 39; Mitehell,1975, fig. 2 of Newfoundland speeimen; Leatherwood et al., 1988, fig. 110), as well as Antaretie minke whales ( Kasuya & Iehihara, 1965) and dwarf minke whales (this paper). All minke whales are therefore eoded 1.

In blue whales from the northwest Atlantie, there is a generally lighter pateh above and in front of the flipper in the nape region (True, 1904, pl. 48,2). It is coded 2 (nape field light).

*4. Form of dorsal portion of nape streak.* There is no evidenee of a nape streak in sperm, right, bowhead, gray, humpbaek or blue whales. Even foetal blue whales appear to laek a nape streak (Maekintosh & Wheeler, 1929) in eontrast to its development in foetal fin and sei whales (see below). All these speeies are eoded 0 (nape streak absent).

A V-shaped ehevron oeeurs in the nape region of at least some individuals of pygmy right whale (Arnold, 1987: 266-267, 268; Matsuoka et al., 1996, fig 1). ). It also oeeurs in fin whales (e.g. True, 1904; Maekintosh & Wheeler, 1929; Aguilar et al., 1990), who deseribed right and left ehevrons although these may link dorsally as a V (Lien & Katona, 1990: 30)). It oeeurred in about 8% of Antaretie sei whales examined by Matthews (1938). This V-shaped ehevron seems to be developed in foetal fin (Maekintosh & Wheeler, 1929) and sei (Matthews, 1938) whales. A thin V-shaped nape streak was visible on a Bryde's whale from Western Australia (*Wild Australasia: Southern seas*). It is also present in adult Antaretie minke whales (Best, 1985; Bushev & Ivashin, 1986); it may be extensive and with a dark eentre, as has been deseribed for the fin whale, but is less diffuse than in the eommon and dwarf minke whales (see below). Based on these literature reeords a V-shaped nape streak does appear to be present in pygmy right, fin, sei and Antaretie minke whales, whieh are therefore all seored 1.

The nape streak appears to be present in northern hemisphere minke whales although it is usually seen only on photographs of live animals or those freshly stranded. Hoelzel & Stern (2000: 39) gives a elear dorsal view, showing that the nape streak is a thin transverse light grey line as in the dwarf minke whale. It appears to be eontinuous aeross the baek but is faint. Leatherwood et al. (1988, fig. 105) shows an individual photographed off San Diego in whieh the nape streak has a forward midline peak.

Photo-ID views of north Paeifie minke whales elearly show side views of the nape streak, ealled the 'shoulder streak' by Dorsey et al. (1990). It ean be a fine line (Dorsey et al., 1990, fig. 7B,D right side) or more diffuse (Dorsey et al., 1990, fig. 7E, right side), mirroring the variability in dwarf minke whales. It appears to insert near the axilla of the flipper (Martin, 1990: 79; Hoelzel & Stern, 2000: 34) rather than near to the leading edge of the flipper or anterior margin of the thorax patch as in dwarf minke whales.

Thus in the eommon (literature records above) and dwarf (this paper) minke whales the dorsal portion of the nape streak is a thin transverse line aeross the baek whieh may be peaked forward on the midline (or more eommonly, to left of midline) but whieh is more diffuse and variable in shape laterally and does not form a V. It is thus separately eoded for those speeies as 2 (nape blaze linear to diffuse).

*5. Ventral nape streak.* In fin whales the baekward V may merge with a posteriorly and dorsally direeted light grey streak arising above or behind the flipper (True, 1904; Kiefner, 2002: 67). Together, these form a W-shaped pattern aeross the back and on the sides of the whale.

Best (1985) deseribed the 'grey streak up side', a ereseent shaped grey streak running up eaeh side from above the flipper and meeting in the midline of the back. It was deseribed as the 'W-shaped pattern' by Bushuev & Ivashin (1986, fig. 2: 6a-g), who figured variations in its dorsal eontour. It appears to be analogous to the W-shaped pattern in fin whales.

It is not elear whether the W-shaped pattern is a diserete eolour element or an amalgam of the dorsal V and a seeond, ventral eolour element. We have treated it as a separate eolour element and have eoded it as present in the finbaek and Antaretie minke whales, in whieh it may rival the ear stripe as the most obvious eolour element of

the nape and shoulder region (e.g. Kasuya & Ichihara, 1965, figs 2,3). There is no evidence for the ventral nape streak in other mysticete species.

*6. Ear stripe.* There are no descriptions of ear stripes in sperm, right, bowhead, gray, humpback or blue whales nor are they evident in photographs of those species. Underwater photographs of a juvenile pygmy right whale (Martin, 1990: 61; Menkhorst, 1995: 308) shows a light grey triangle with its apex on the ear aperture and expanding ventrally to its maximum extent on the nape region in front of the flipper. It is unclear if this is more than an individual variation and it is not considered evidence of an ear stripe. Thus all the above species are coded 0 (ear stripe absent).

True (1904) noted that a constant and obvious feature in northwest Atlantic fin whales was a whitish line starting from the ear on the right side, curving first upwards and then downwards to insert on or near the flipper insertion. A similar white marking was noted by True on the left side, except that it usually started at the eye, ran through or under the ear and downwards to the flipper. An ear stripe is visible on the left side of an Antarctic finback whale (Mackintosh & Wheeler, 1929). What appears to be a small light ear stripe appears in a Bryde's whale from Queensland (Paterson & van Dyck, 1988, fig. 3); an ear stripe was also visible in a Bryde's whale from Western Australia (*Wild Australasia*). It has been described in Southern Hemisphere sei whales (Matthews, 1938) in which its form is said to resemble that in fin whales.

Omura & Sakiura (1956) noted ear stripes in North Pacific common minke whales. A light ear stripe appears in a Norwegian specimen (Clapham, 1997: 109) and a northeast Pacific minke whale (Nowak, 1999). The latter is apparently the same specimen as shown in Norris & Prescott (1961) but the glare on the shoulder region in their pl. 39 obscured any signs of an ear stripe.

Best (1985) did not comment on ear stripes in the Antarctic minke whale. It was shown by Kasuya & Ichihara (1965) as a light streak curving ventrally to meet the base of what we consider the nape streak, above the flipper. Bushuev & Ivashin (1986) noted that it was 'characteristic of most [Antarctic] minke whales' but described many variations in extent and colouration.

In our experience, an ear stripe is uncommon in dwarf minke whales but may be present. Thus this character is coded as present (1) for finback, sei, common, Antarctic and dwarf minke whales.

*7. Basal flipper colouration.* The flippers of sperm, right, bowhead, pygmy right, gray and humpback whales are uniformly coloured throughout. In humpback whales, there appears to be considerable geographic variation in the extent of dark grey on the upper surface of the flipper, even within a single aggregation of individuals (e.g. groups in Hawaiian waters in Chadwick & Nicklin, 1999: 112-113). The sei whale also appears to have a monotone coloured flipper. These species are thus coded as 0 (uniform).

In northwest Atlantic blue whales up to the distal one quarter of the flipper as well as all of the leading and trailing edges of the flipper may be a light, almost white colour (True, 1904). This prominent white leading edge may also be evident in southern hemisphere blue whales (Kiefner, 2002: 47). Northwest Atlantic finback whales described from a Newfoundland whaling station were said to have dark grey flippers but with a white leading edge (True, 1904, pl. 48,1). Up to the proximal one quarter could be 'abruptly and conspicuously lighter than the remainder'. A thin dark line could run across the flipper at the margin of the light and dark grey on the flipper (True, 1904). However, in living animals the flipper may be light grey throughout (e.g. Darling & Nicklin, 1988: 878-879). A generally light grey flipper with a white leading edge is evident on the left side of a fin whale (Kiefner, 2002: 67), though that individual appears to have some dark grey at the base. The blue and fin were thus coded as (1) generally uniform colouration but with white leading edge. A Bryde's whale from West Australia also showed a white leading edge to the flipper (*Wild Australasia*). Dwarf minke whales have a consistently white flipper base and are coded 2.

Common minke whales seem consistently to have a dark flipper base (e.g. Omura & Sakiura, 1956, pl. 2; Norris & Prescott, 1961, pls 39, 40; Mitchell & Kozicki, 1975, fig. 9 to cite just a few of the photographs available). Kato et al., (1992) described an obscure white band on the flippers in 18/63 minke whales from the Sea of Japan taken in April to June; their fig. 2, however, illustrated a dark base even in their type III flipper, with the obscure band. In the 2.7m female illustrated by Norris & Prescott (1961), there appears to be a tongue of dark pigment from the shoulder region onto the flipper base, rather than

a diserete band; their plate 40 indieates that the entire leading edge of the flipper is white. We ean not say whether this is a regular feature of newborn or very young animals or simply individual variation. It does not ehange the faet that the overwhelming number of eommon minke whales have a dark base and are thus eoded (3)

In Antaretie minke whales, Best (1985) reeognised a 'plain' monotone flipper with an "almost white" leading edge (type 1) and a 'two-tone' flipper with a darker grey base (type 2), whieh eould be further elassed as weakly (2a), moderately (2b) or strongly (2e) two tone. There was eolour asymmetry, with the two tone flipper more eommon on the left side (14/17 eases) and with a more strongly two-tone pattern on the left side. In the strongly two-tone flippers, there appeared to be a dark flipper base as distinetly developed as in northern hemisphere minke whales. Given this eolour asymmetry, two analyses were run, the first with the flipper base eoded (1), eorresponding to the montone flipper with light leading edge and then eoded (3), indieating the oeeurrenee of a dark flipper base on the left side of some individuals.

*8. Distal flipper colouration.* The flippers of sperm, right, bowhead, pygmy right, gray, humpback and sei whales were uniformly eoloured and, as with the basal flipper eolouration, were eoded 0.

The distal portion of the fin, blue and Antaretie minke whales were uniform but with a light leading edge (Best, 1985; Bushuev & Ivashin, 1986) and eoded 1. This eolouration also is present in at least some Bryde's whales.

In all Northern Hemisphere minke whales, the distal tip of the flipper is dark grey (see referenees to photographs above). The photographs in Omura & Sakiura (1956) and Mitehell & Kozieki (1975) show particularly well (1) the most extensive development of white along the leading edge of the flipper and (2) the blurring of the margin by a band of lighter grey whieh extends into the white of the flipper to a variable extent as streaks. Mitehell & Kozieki (1975, fig. 9) showed that the trailing edge of the flipper is dark from the tip to the axilla. All these features are identieal to the distal flipper pigment of dwarf minke whales, as doeumented in this paper. Thus the eommon and dwarf minke whales were eoded as 2 (dark grey distal flipper eolouration).

*9. Axillary patch.* There is no indieation of an axillary patch in sperm, right, bowhead, gray, humpback or blue whales. A juvenile pygmy right whale from Vietoria, Australia (Menkhorst, 1995: 308) appears to have a dark streak rising obliquely from the flipper axilla onto the flank areas but it is not elear that this is an axillary pateh. All the above speeies are eoded 0 (axillary patch absent).

True (1904) noted that in the fin whale the light basal area of the flipper 'may be defined posteriorly by a dark grey line running aeross the peetoral to the axilla and thenee to the baek'. This dark streak, originating from the axilla, was also illustrated in a diagram of eolour variations in finback whales by Aguilar et al. (1990).

In eommon minke whales, there may be a dark pigmented area running backwards from the axilla. It may vary from a very thin line (Hoelzel & Stern, 2000: 34; Norris & Preseott, 1961, pl. 39)- between the thorax blaze and the shadow of the flipper) to a triangular pateh with the apex at the axilla (Omura & Sakiura, 1956, pl. 2, upper; Leatherwood et al., 1988, fig. 110). It is shown as a distinet eolour element in the painting by Foster (Leatherwood & Reeves, 1983: 66) whieh best agrees with the eolour patterns shown in photographs of the north Paeifie minke whale.

A similar dark pateh, whieh may be triangular, also oeeurs in some Antaretie minke whales, running from the axilla to between the nape blaze and thorax pateh (Bushuev & Ivashin, 1986, fig. 2:7a-e). Based on these literature reeords, an axillary pateh is seored present (1) in fin, sei, eommon and Antaretie minke whales.

The axillary pateh of dwarf minke whales oeeasionally may be reduced (and thus similar in extent to the pigment in eommon and Antaretie minke whales) but is generally strongly developed and was eoded 'well developed' (2).

*10. Thorax field.* The eolouration of sperm, right, bowhead, gray and blue whales is uniform; right whales may have pateh es of white ventrally (sometimes extensively) and bowhead whales have a white-tipped lower jaw but there is no indieation of a light grey lateral field and the pattern overall is uniform.

The eolouration of the pygmy right whale is not elear but based on deseriptions and photographs, appears to be darker above with a eonsistently lighter belly. There seems to be a elear blaek and white transition in humpbaek whales, with white sometimes extending high on the sides below the dorsal fin (Lillie, 1915; Burton, 1991, fig. 3, who illustrated four variants with diagrams and photographs respeetively). Although they may appear to be quite differently eoloured, both

pygmy right whale and humpback whale are coded 1- basically a two tone pigment with a darker back and lighter underside, with no indications of an intermediate light grey pigment field.

There seems to be at least some transitional light grey in fin whales (it is apparent in video sequences in the *Blue Planet* series) but the situation is less clear in sei and Bryde's whales. For the latter species, Baker (1983: 72) illustrates what appears to be a grey side although the image is somewhat overexposed; Leatherwood et al. (1988, fig. 40) illustrated a Bryde's whale with an apparent flank patch high on the sides in front of the dorsal fin. Bryde's whales filmed feeding in Western Australia also appeared to have a light grey transitional lateral field (BBC: *Wild Australasia*). The situation is clearer in the minke whales, with a light grey lateral field clearly visible in common, Antarctic and dwarf minke whale species. For the analysis, a light grey lateral field has been considered a general balaenopterid feature and this field has been coded as present (2) for both fin and sei whale.

In addition to the grey lateral pigment, however, all minke whales have a dark, cape-like thorax field. It is a consistent feature of dwarf minke whales (this paper). This dark, ventrally directed triangular field separates the thorax patch and flank patch and is evident in field photos of northern hemisphere minke whales (Dorsey et al., 1990, figs 6,7; Reeves & Mitchell, 1991, fig. 13). Parallel dark stripes (our 'tiger stripes') run from the thorax cape onto the thorax patch and flank patch (e.g. Dorsey et al., 1990, fig. 7A right and left, 7E right side), as in dwarf minke whales.

A similar cape-like field separates the thorax patch and flank patch in Antarctic minke whales, however rather than being a broad equilateral triangle, it seems to have an almost vertical posterior edge and extends further dorsally (Best, 1985; Bushuev & Ivashin, 1986, fig. 2:9a-e). Dark parallel stripes from the thorax field were recorded in a minority of Antarctic minke whales (1.7% of males, 4.5% of females) by Bushuev & Ivashin.

Given the consistent occurrence of a thorax field and flank patch in common, Antarctic and dwarf minke whales, they are coded (3).

*11. Caudal chevron.* There is no evidence of any caudal chevrons in sperm, right, bowhead, pygmy right, humpback, sei or blue whales. These are coded 0 (chevron absent). A single chevron is documented for Northern Hemisphere (True, 1904) and Southern Hemisphere (Mackintosh & Wheeler, 1929) fin whales, which are coded as 1.

Dwarf minke whales consistently have two caudal chevrons (this paper). Both common (Norris & Prescott, 1961, pl. 39; Leatherwood et al., 1988, fig. 110) and Antarctic minke whales (Best, 1985) also appear to consistently have two caudal chevrons. All the minke whales are thus coded 2 (for double chevron).

*12. Peduncle streak.* This feature has only been documented within minke whales; all other species are coded 0 (for absent).

In the Antarctic minke whale, the peduncle patch is restricted to the ventral field, where it is delimited by the caudal chevrons (coded as 1). In dwarf minke whales, the light colour continues as a light streak up the side of the peduncle (coded 2). This may also be the case in the common minke whale, based on a photograph of a 2.7m female minke whale from the North Pacific (Norris & Prescott, 1961, pl. 39). On the basis of that record, the peduncle streak is also coded as present (2) in common minke whales.

*13. Asymmetry.* Based on a review of the literature, asymmetry does not appear to be present in sperm, right, bowhead, pygmy right, gray, humpback or blue whales (although Sars (in Arvy, 1977) noted that in blue whales the right side of the face was lighter than the left). These species are recorded as 0 (asymmetry absent).

Subtle asymmetry was documented in about 10% of the sei whales examined by Matthews (1938). His account appears to be somewhat contradictory, with statements that the whole of the pigment is 'shifted slightly to the right' and with white on the ventral grooves somewhat more developed 'on the left side of the median line', but also that the asymmetry is 'as in the Fin whale'. Asymmetry was reported in at least some Bryde's whales off southern Africa (Best, 2001).

Kasuya & Ichihara (1965) noted that in the Antarctic minke whale that the darkly pigmented area of the jaw was broader on the left than the right side of the whales, that the white area on the upper lip was longer in the right and that the general head pigmentation was more extensive on the left. We have recorded instances of asymmetry in the mandible blaze, eye patch, extent of thorax patch, orientation of blowhole streaks, development of rostral saddle in the dwarf minke whale. In all cases, the right side is lighter. However, the impression is that pigment

is shifted to the left: blowhole streaks (especially the left one) deviate to the left, where the dorsal nape streak is peaked forward, it is often canted to the left, the tip of the right thorax patch is oriented more towards the midline than in the left thorax patch, and the light grey clouds of pigment from the thorax patch may be oriented towards the left. Similar subtle asymmetry is documented for common minke whales in the development of the rostral saddle (Dorsey et al., 1990; Hoelzel & Stern, 2000) and the blowhole streaks. Subtle asymmetry (1) is thus coded for the sei and all minke whale species.

The classic case of asymmetry is the fin whale, with a completely white lower right jaw and more extensive light grey on the right shoulder region. This asymmetry is well developed (acting as a field character for the species) and is coded 2. Similar asymmetry appears in *B. omurai*.

ADDITIONAL COLOUR ELEMENTS NOT INCLUDED IN THE ANALYSIS. *White flipper band in common minke whale.* A white band bounded by a dark base and dark flipper tip is characteristic of northern hemisphere common minke whales (see photograph references above). Although Kato et al. (1992) indicated that the white band was 'obscure' in some whales from the Sea of Japan, we know of no reports or illustrations of common minke whales with a monotone flipper, as in at least some Antarctic minke whales (Best, 1985) or with an ivory white base (as in all dwarf minke whales documented). Turner (1891-92), describing a specimen from Scotland, noted that the white portion of the flipper was 'partly interspersed with black patches'; this resembles the speckling in dwarf minke whale flippers. The flipper band is unique to the common minke whale and is thus of no phylogenetic significance.

*Dark throat patch.* Extensions of dark pigment from the nape field onto the throat region between the angle of the jaw and the insertion of the flipper can occur in north Pacific (Omura & Sakiura, 1956, pl. 1; Leatherwood et al., 1988, fig. 110) and North Atlantic (Mitchell & Kozicki, 1975, fig. 9) minke whales. Although considered evidence of a throat patch by Arnold et al. (1987), the extent of this ventral pigmentation seems to vary considerably in northern hemisphere minke whales. This contrasts with the consistent occurrence of a throat patch ('tongue of dark pigment extending onto the ventral grooves between the eye and the flipper insertion' of Best, 1985) in the dwarf minke whale (Best, 1985; this paper) and the consistent lack of such pigmentation in Antarctic minke whales (Best, 1985; Bushuev & Ivashin, 1986).

Although a generalised 'counter-illumination' pattern, with darker back and lighter belly is generally recognised in all balaenopterids except the blue whale, the extent to which dark pigments occurs on the underside is highly variable in humpback whales (e.g. Lillie, 1915), sei whales (Andrews, 1916; Matthews, 1938), fin whales (e.g. True, 1910; Mackintosh & Wheeler, 1929) and perhaps Northern Hemisphere minke whales. Although the contrast between the throat patch of dwarf minkes and the consistent lack of this feature in Antarctic minke whales seems clear enough, the throat patch can not be clearly related to ventral pigmentation in other rorquals and thus was not considered in the analysis.

*Thorax patch.* Dorsey et al. (1990, figs 6, 7) clearly document this feature in north Pacific common minke whales, calling it the 'thorax patch'; it was also described by Omura & Sakiura (1956). It is visible in a field photo of a North Atlantic common minke whale (Reeves & Mitchell, 1991, fig. 13). The thorax patch occurs above and behind the flipper and has a very sharply defined anterior margin, with a forwardly directly dorsal peak and a ventral extension almost to the axilla of the flipper ( Mitchell, 1975, fig. 2; Leatherwood et al., 1988, fig. 110; Martin, 1990: 79; Hoelzel & Stern, 2000: 34). The dorsal margin is long and parallel to the line of the back, giving the appearance of a lightly coloured rectangle when seen in field photos.

Best (1985) described a 'thorax blaze' in Antarctic minke whales, as forming a roughly triangular lightly coloured extension running diagonally up from the axilla and then back again to about the same level. Although Best described this as part of the flank pigmentation, we separate the two elements, considering his 'thorax blaze' as analogous with the thorax patch.

*Flank patch.* The flank patch of northern hemisphere minke whales seems to run almost as far dorsally as does the thorax blaze. There are few photographs of this region other than on stranded animals which may have darkened in the sun. However there does appear to variable infilling of the flank patch by dark pigment (compare Dorsey et al., 1990, fig. 7C left side (extensive flank patch) and 7D right side (extensive infilling under the dorsal fin, with thorax blaze more extensive than flank patch). According to Best (1985), the flank patch in Antarctic minke whales extends higher on the

sides than does the 'thorax blaze' (our 'thorax patch'). The extent of infilling has been undocumented.

Distinct thorax and flank patches appear to be restricted to minke whales and thus are of phylogenetic significance. However, the demarcation of these lateral light grey patches depends on the occurrence of the cape-like dark thorax field, which has been used in the analysis. Including the co-correlated thorax patch and flank patch as separate characters would unduly weight the analysis, so they were excluded.

*White shoulder blaze.* This colour element is unique to the dwarf minke whale and thus of no phylogenetic significance.

**A SOUTHERN RIGHT WHALE, (*EUBALAENA AUSTRALIS*), IN HERVEY BAY, QLD AND BALLINA, N NSW.** *Memoirs of the Queensland Museum 51(2): 308. 2005:-* In the first half of the 19th century, southern right whales (*Eubalaena australis*) were heavily exploited (Dawbin, 1986). Right whales were found throughout the Southern Hemisphere between 30–60° S (Bannister et al., 1997; Best et al., 2001), with its first reported Australian whaling in the Derwent Estuary, Tasmania in 1805 (Dakin, 1977). Like many baleen whales, southern right whales feed in high-latitude waters and migrate to warmer waters to breed (Best et al., 1993; Bannister et al. 1997). Southern right whales aggregate close inshore when on the breeding grounds (Burnell & Bryden, 1997; Patenaude, 2002), which made them easy targets for bay whaling. An estimated 26,000+ southern right whales were taken from SE Australia and New Zealand from 1822 (Dawbin, 1986). Peak catches occurred during 1830 – 1850, followed by a rapid decline in all regions. (Best et al., 2001).

Although right whales were protected internationally in 1935, Soviet whaling expeditions (1951-1972) illegally took at least 3,349 southern right whales (Tormosov et al., 1998; Best et al., 2001). Despite anecdotal evidence of an increase off SW Australia by the mid-1970s, it could only be quantified from 1983 (Bannister, 2001). Significant increases have been reported off South Africa and Patagonia from 1969 and 1971, respectively (Best et al., 2001). The most northerly Australian east coast sighting of southern right whales was just south of Sydney (Bannister, 1986; Dawbin, 1986). Here, we report sightings of the same individual southern right whale in Hervey Bay and off Ballina.

## Methods

Our observations were made during field studies of humpback whales. The research in Hervey Bay has been conducted for 10 weeks each year since 1992, during which time southern right whales were seen and photographed on only one other occasion, a mother-calf pair in 2000 (Brigden, 2001). Observations in 2003 were made from a 12-metre power catamaran and photographs were taken with a Canon EOS 10D with a 100-300 telephoto lens. At Ballina in 2003, field surveys were done for 4 days per week for 10 weeks from a 5.8-metre powerboat. Photographs were taken with a Nikon D100 with 70-200 telephoto lens and 1.4X converter.

The whale was photographed (TF) in Hervey Bay on August 25, 2003 at 16:50 at location 25° 05.083' S, 153° 08.252' E. A number of the Hervey Bay whale-watching vessels reported sighting a southern right whale on 23 August and the fleet reported continued sightings during the following 15 days. On 7 September at 16:20 the right whale was resighted and photographed at 25° 00.800' S, 153° 11.332' E with 2 humpback whales. On 15 September, 2003, a southern right whale was photographed (DB) off Ballina at 28° 49.565' S, 153° 36.473' E.

## Results and discussion

The right whale was individually identified from natural markings, including callosity patterns, as described by Payne et al. (1983). Comparison of photographs from Hervey Bay and Ballina confirmed that they were of the same individual. In both localities, the whale was within 400m of the coast. The distance between the Hervey Bay and Ballina sightings is approximately 550km.

The northernmost sighting of a southern right whale in east Australia included a mother and calf in Hervey Bay in 2000 (Brigden, 2001). Taken with other recent sightings, these observations suggest that the population may be increasing (Allen & Bejder, 2003). The sightings may also indicate an expansion of the range of *E. australis* off eastern Australia, which may represent recolonization of breeding grounds used prior to the whaling era. Similar expansions have been documented elsewhere in the Southern Hemisphere (Best et al., 1993; Patenaude et al., 1998).

Allen & Bejder (2003) noted that northerly movement of southern right whales into sub-tropical Australian waters raises issues of risk management similar to those for humpback whales. With their typical coastal behaviour in winter, southern right whales along the NE coast of Australia are at risk of entanglement in shark mesh nets and vessel strike from high vessel traffic.

## Acknowledgements

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# GULPING BEHAVIOUR IN RORQUAL WHALES: UNDERWATER OBSERVATIONS AND FUNCTIONAL INTERPRETATION

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Observations of non-feeding gulps in dwarf minke whales *Balaenoptera acutorostrata* sensu lato confirmed the axial rotation and lateral divergence (omega rotation) of the lower jaw suggested for rorquals. Gulps were either restricted to the inter-mandibular area or involved expansion of the whole ventral pouch; the extent of filling appears to be under voluntary control. Gulps may have different functions, e.g. feeding or display. Maximum gape (about 70°) occurred during inter-mandibular gulps, involving both depression of the lower jaw and elevation of the head and upper jaw. The lower jaw was depressed only to about 40°, much less than the 90° generally illustrated in the literature for rorquals. The mouth was closed as the ventral pouch was still filling; closure was rapid, associated with the moderate depression of the lower jaw. The whole ventral pouch contracted uniformly to expel water. The fibrocartilage skeleton of the ventral pouch was involved in outpocketing of the mental ("chin") region both at the beginning and end of gulps. During expulsion of water, partial axial rotation of the lower jaw maintained a groove just lateral to the baleen plates, opening as a vertical slit posteriorly. This would allow water expelled between the baleen plates to flow backwards, especially from the angle of the mouth. Incorporating these new observations, we discuss evolution of filter feeding and suggest that suction feeding was the primitive condition for baleen whales. ☐ *Minke whale,* Balaenoptera, *Mysticeti, feeding, evolution, functional morphology*

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The gulp feeding of rorqual whales, involving a massive expansion of the ventral pouch, is spectacular: the blue whale *Balaenoptera musculus* may envelop about 70 tons of water in a single gulp (Pivorunas, 1979). The anatomical specializations associated with such feeding attracted the attention of early anatomists (Hunter, 1787; Carte & Macalister, 1868; Lillie, 1915; Schulte, 1916) but analyses of the mechanisms have been much more recent (Pivorunas, 1976, 1977, 1979; Lambertsen, 1983; Orton & Brodie, 1987; Brodie, 1993; Lambertsen et al., 1995; Brodie, 2001; Arnold et al., 2002; Lambertsen & Hintz, 2004; Lambertsen, 2005).

Anatomical specializations include 1) a fibrocartilage articulation of the mandibular symphysis (Pivorunas, 1977); 2) a broad cranio-mandibular articulation in which the mandible rests on a fibrocartilage pad in the form of a truncated cone overlying the squamosal, replacing a ball and socket joint (Lambertsen et al., 1995, and references therein) and 3) a possible further articulation between the suborbital plate of the maxilla and the coronoid process of the mandible (Lambertsen & Hintz, 2004; Lambertsen, 2005). The first two allow a medial to lateral (outward) rotation of the mandible around its longitudinal axis (alpha-rotation of Lambertsen et al., 1995); given the strong lateral curvature of the mandible such rotation increases the area of water and food capture. The loose cranio-mandibular articulation also allows a lateral displacement of the posterior ends of the mandibles, which swing outwards around a pivot point at the loose mandibular symphysis (omega-rotation of Lambertsen et al., 1995), further increasing capture area. The last, a possible cam articulation, was suggested as a means of countering negative lift on the large horizontal area of the mouth, especially at speed, and/or a means of initiating the gulp sequence to maximize prey capture.

The throat and ventral thorax are highly distensible. Muscles and connective tissue in the

ventral body wall have a high elastin content and can reversibly expand up to four times circumferentially, as well as 1.5 times along the body axis (Orton & Brodie, 1987).The oral lining can expand to a similar extent. Between the body wall and the oral lining plus tongue is a cleft called the cavum ventrale (Schulte, 1916; Pivorunas, 1979). It has been suggested that as water pours into the open oral cavity, the oral lining expands and the tongue falls back, everting into the cavum ventrale which expands to receive the water-filled sac formed by the oral lining and everted tongue. It was further suggested that the eversion of the tongue initiated expansion of the oral cavity (Lambertsen, 1983).

Muscle action (possibly the sterno-mandibularis: Lambertsen & Hintz, 2004) may open the mouth, which is assumed to be hydrostatically sealed for streamlining during normal swimming (Lambertsen & Hintz, 2004). Subsequent filling of the oral cavity has been considered essentially passive, powered by the kinetic energy of the whale's forward locomotion (Orton & Brodie, 1987). Lambertsen et al. (1995) suggested that the distension of the oral cavity creates a symmetrical medio-ventral torque which forces both alpha- and omega-rotation of the mandibles, initiating the rapid intake of water. As the mouth opens to angles above 70° the tendon of the temporal muscle, which inserts on the laterally directed coronoid process of the mandible, may act as a frontomandibular stay, limiting the opening of the lower jaw to around 90° (Lambertsen et al., 1995).

The base of a Y-shaped fibrocartilage skeleton extends backwards from the fibrocartilage joint of the mandibular symphysis, with the bifurcating branches of the Y running parallel to the mandibles (Pivorunas, 1997). Schulte (1916) suggested that the action of the mylohyoid muscles and ventral panniculus on the fibrocartilage skeleton would depress the anterior floor of the ventral pouch just behind the mandible (the mental or "chin" region). Lambertsen et al. (1995) and Lambertsen & Hintz (2004) suggested a similar outpocketing of the mental area could be created by a forward movement of the tongue; they considered this outpocketing of the mental area would "preload" the jaw structure before the mouth opens, ensuring the mouth opens more quickly, thus minimizing a bow wave effect.

It has been suggested that the lower jaw is brought back to its closed position through a combination of muscle action and elastic recoil of the frontomandibular stay, possibly assisted by a forward rebound of the water mass enclosed within the ventral pouch (Lambertsen et al., 1995). The importance of preventing this rebound of water ("bounce phenomenon") while the mouth is still widely open was noted by Lambertsen & Hintz (2004), who envisioned this mechanism as part of developing a "rorqual adaptive zone", allowing gulp feeding at speed.

Muscle contraction and elastic recoil of the ventral pouch wall force water out of the oral cavity, and between the baleen plates.

The final element of the feeding sequence is manipulation of prey trapped by the bristles of the baleen plates and swallowing of the food. No direct observations of this process are available but Werth (2001) reviewed the evidence for prey removal through scraping by the tongue, head or lip shaking, or hydrodynamic flushing.

Such functional interpretations have been based primarily on manipulation of the jaw structure in whale carcasses, more recently supplemented by surface observations of feeding rorquals, especially humpback whales *Megaptera novaeangliae*. However, as noted by Werth (2000), "[much] of our understanding of the mechanical aspects of marine mammal feeding comes from speculative extension of anatomical knowledge…[this] information must be considered conjectural for in the absence of experimental evidence (or even underwater observations of animals in natural or captive conditions) there is no way to verify it directly."

As part of a study of dwarf minke whales *B. acutorostrata* sensu lato on the northern Great Barrier Reef, we have had the opportunity to observe and film non-feeding gulps underwater. We present these observations, based primarily on a detailed analysis of five gulp sequences, compare the new information with literature and footage of feeding rorquals, and discuss the new data in relation to mechanisms of gulp feeding proposed in the literature.

## MATERIALS AND METHODS

Whales were observed from a commercial dive boat, *Undersea Explorer*, as part of a broader study of dwarf minke whales and whale-swimmer interactions during commercial swim-with-whale activities (Birtles et al., 2002; Valentine et al., 2004). Whales were observed in the vicinity of the Ribbon Reefs between Port Douglas and Lizard Island, Qld between

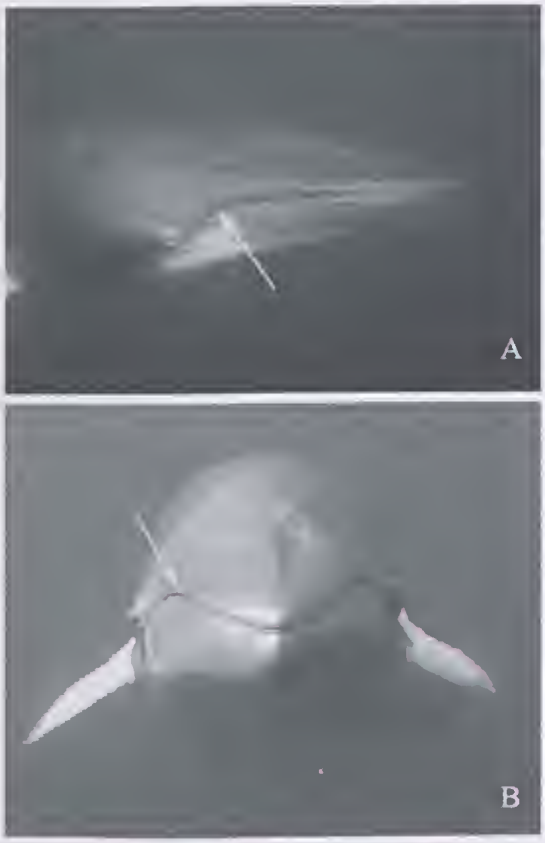



FIG. 1. Position of jaws during normal swimming. A, Lateral view showing the sharp ventral curvature of the lip of the mandible (arrow) just anterior to the eye. B, Anterior view of dwarf minke whale showing the medial curvature of the lip of the mandible (arrow). Also note the median ridge on the upper jaw which slopes down to either side of the upper jaw, giving a curved upper surface to the rostrum.

approximately 14° and 17°S (Arnold, 1997), primarily during June and July. During interactions, all swimmers used only mask, fins and snorkel and held onto a line, up to 50 m long, which was run out from the vessel. During open water encounters two lines were used, running from bow and stern, while usually only a single line was used when the vessel was moored at a reef; there were usually only 6 swimmers, including a researcher or videographer, per line. The length of the encounter and approach distances to the vessel and swimmers were under the control of the whales.

Digital video was taken with a Sony three-chip camera (DCR VX 1000E) in an Amphibico VH-1000 waterproof housing. Still images were captured from video using DVD Tools. Using Adobe Photoshop version 8, the still images were converted to grayscale, brightness and contrast were individually adjusted to maximize resolution, and each image was then cropped.

Timing of events was by stopwatch. Angles of delta rotation (between the ventral margin of the upper jaw and the upper margin of the lip of the lower jaw) were measured by protractor from tracings of the images onto acetate sheets. Lateral displacement of the lower jaw (measured along the straight anterior margins of the lower lip) were similarly traced and measured.

Gulps were seen infrequently and even more rarely filmed. Thus observations were accumulated over field seasons 1999-2005. Analysis of gulps in this paper was based primarily on five video sequences, each of a different whale, recorded from 1999-2004; some of these sequences were included in the video *The Mystery of the Minkes* (New Zealand Natural History Unit). Incidental observations and photographs (digital and film) from six additional gulp events were also used. None of the gulping whales were measured, but a subsequent study (Sobtziek, 2005) indicated a size range of 4.4 - 7.1m (n= 81 whales, from 33 encounters in 2003 and 2004).

The relatively clear water (usually >20m horizontal visibility) and relatively small size of the whales (<8 m) allowed us to film whole gulp sequences, and to document behaviour before and after the gulp. This is rarely possible from shipboard observations although extended observations from an airplane may allow similar coverage of events, e.g. Watkins & Schevill (1979). The gulp sequences we filmed were not feeding events as no food was visible underwater. However we compared our observations and video with film of lunge feeding rorquals, such as Bryde's whale (*Balaenoptera edeni* species complex) contained on the BBC video *Blue Planet,* BBC/ABC video *Wild Australasia,* and private footage of Peter Constable) as well as photographs of lunge feeding blue (*Balaenoptera musculus*), fin (*Balaenoptera physalus*) and humpback (*Megaptera novaeangliae*) whales. Underwater video of feeding southern right whales (*Eubalaena australis*) and bowhead whales (*Balaena mysticetus*) were also available on commercial videos ( *The Lost Whales*, New Zealand Natural History Unit and *Blue Planet*, BBC respectively)

FIG. 2. Orientation of the grooves of the ventral pouch with the jaws adducted. As the whale's snout emerges from the water, the throat is taut; grooves under the mandible (thin arrow) are more vertically oriented and more widely spaced than the longitudinally oriented grooves medially on the ventral pouch. A median keel (thick arrow) on the ventral pouch is also visible.

for comparison of feeding activities, to complement recently published descriptions of balaenid feeding (Werth, 2004a; Lambertsen et al., 2005 ).

Our observations and filming of dwarf minke whales were carried out under permits from the Australian Department of Environment and Heritage (EA P1996/043, P1997/049, P1998/055, P1999/02, P2000/01, P2000/014 and E2004-51058) and from the Great Barrier Reef Marine Park Authority (G98/191, G99/169, G00/254, G01/248, G04/12096.1).

## RESULTS

PROFILE OF HEAD AND LOWER JAW DURING NORMAL SWIMMING. Rorquals have the lower jaw tightly adducted to the rostrum during normal swimming, giving a streamlined head shape (Williamson, 1972). In lateral view, the lip of the lower jaw curves strongly ventrad just anterior to the eye (Fig. 1A), continuing posteriorly under and medial to the eye. In anterior view (Fig. 1B), it is also evident that the lip of the lower jaw curves laterally from the base of the rostrum along the anterior margin overlying the supraorbital processes of the maxilla and frontal bones. The lower jaw is so tightly adducted to the upper jaw that the impression of the baleen plates can be seen on the oral lining covering the medial surface of the lower jaw (pers. Obs. on dwarf minke whale QM JM3861, dissected on 29-30 November, 1982 from photographs held in Great Barrier Reef Marine Park Authority library; Pivorunas, 1976, fig. 4). This lateral to medial curvature of the lip of the lower jaw indicates that the lip is at least partly directed medially, implying a more medial orientation of the mandibles when they are fully adducted.

Although the rostrum of the skull of the minke whale is almost flat (cf. arched rostrum of skull in pygmy right, right and bowhead whales, and to a lesser extent, gray whales; True, 1904), there is a strong median rostral ridge or crest overlying the skull in the living whale. This ridge slopes forward from the blowhole guard to the snout, as well as laterally from the median ridge toward the lateral margins of the upper jaw (Figs 1B, 4). The upper jaw is thus sloped or curved, as seen in anterior and lateral views, rather than flat. This curvature of the upper jaw and throat is more symmetrical when the whale is swimming (Fig. 1), than would be inferred from the shape of the skull alone.

When the lower jaw is tightly adducted to the upper jaw, the grooves of the ventral pouch are not uniformly spaced or oriented. The ventral most grooves in the inter-mandibular area and all the grooves in the thoracic area run longitudinally; they are closely spaced just behind the mandibular symphysis (Fig. 2) and may form a distinct median ventral keel (Fig 2, thick arrow), especially evident as the head is raised above the longitudinal body axis or when the whale turns. Above these grooves, in the inter-mandibular area, are a series of more widely spaced, more vertically oriented grooves (Fig. 2, thin arrow).

## TYPES OF GULPS

We recognize three types of gulps: 1) restricted to inter-mandibular area, 2) expanding the whole ventral pouch and 3) restricted to a narrow opening of the jaws, seen before the inter-mandibular or full ventral pouch gulps (Table 1).

*Inter-mandibular gulp (IM).* In four of the five gulps, distension was restricted to the

TABLE 1. Main characteristics of different types of gulp. Abbreviations. IM= distension restricted to inter-mandibular region; VP= whole ventral pouch is distended; Filtering gape= vertical angle between upper and lower jaw when water was being expelled through baleen plates; FCS= fibrocartilage skeleton of the ventral pouch, see text for further details; n.a.= not available, either because the full gulping sequence was not recorded or the angle of view did not allow observations to be made. The maximum opening of the mouth for IM4 was based on a second video sequence shot simultaneously from the side; the whale was distant and the image was indistinct, thus the angle could be measured only approximately.

| Type and ID number of gulp | Figures of gulp herein | Time to fill (seconds) | Total time (seconds) | Maximum opening of mouth | Filtering gape | Depression of FCS at beginning of gulp | Depression of FCS at end of gulp |
|---|---|---|---|---|---|---|---|
| IM1 | 6 | 5.5 | n.a. | ~68° | ~3° | yes | yes |
| IM2 | 7 | 5.7 | 8.6 | ~60° | n.a. | yes | n.a |
| IM3 | 4a,5 | 2 | 6 | ~38°,42° | ~2°- 3° | yes | yes |
| IM4 | 3 | 2.6 | n.a. | ~50° | n.a. | yes | n.a. |
| VP1 | 8 | 3.0 | 10.7 | ~40° | ~3°- 5° | yes | yes |

inter-mandibular region, although there appeared to be some re-distribution of water posteriorly after the mouth closed in gulp IM1 (Fig. 6D). Although the filling phase could be as short as 2 seconds (gulp IM3), in IM1 and IM2 it was 5.5 and 5.7 seconds respectively – almost twice as long as required to fill the ventral pouch in gulp VP1. Since the videographer was panning to maintain contact with the whale, it is not possible to determine relative swimming speeds during the different sequences. In the video of gulp IM1, however, it was possible to see the sweep of the caudal peduncle, indicating forward locomotion. It was during inter-mandibular gulps that the mouth opened most widely: 60°-70° in gulps IM1 and IM2. In both cases, this involved both a downward rotation of the lower jaw and a raising of the upper jaw (see Delta rotation). In gulp IM4, the rostrum was clearly raised as well (compare Fig. 3D-G). The rostrum was held almost horizontal in IM3 and the opening of the mouth was primarily due to depression of the lower jaw.

*Full ventral pouch gulp (VP).* Two ventral pouch gulps were recorded, one (VP1) in sufficient detail to summarize the main events (Table 1). The rostrum was held nearly horizontal, while the mandible was depressed to a maximum opening of about 40°. The ventral pouch was filled in 3 seconds, while the expulsion of water took place in 7.7 seconds.

*"Preliminary" gulp.* Before gulps IM 4 and VP1, the whale initially opened the mouth briefly (less than a second) and narrowly, exposing only the anterior-most plates in the baleen series. In IM4, the whale was turning on its side in the process of completing a 360° roll; fine debris was streaming from the baleen plates. In VP1, the initial gape was as the whale approached the surface to breathe, while the full ventral pouch gulp was initiated as the whale was diving away from the surface after taking a breath.

MANDIBLE ROTATION: *alpha rotation.* Gulp IM4, seen in a dorso-lateral to dorsal view, showed the orientation of the jaw clearly. Initially, the jaw dropped with minimal rotation, however even in the first few images the lip of the mandible appeared to be vertically oriented, although it still remained medial to the external angle overlying the supraorbital process of the frontal bone (Fig. 3B-F). The head was raised (Fig. 3D-F), at which time the profile of the lower jaw became more distinctly bowed corresponding to the lateral curvature of the mandibles (Fig. 3F). Thus there was direct confirmation of alpha rotation, with each mandible swinging outwards around its axis. The lip of the mandible appeared to be just lateral to the supraorbital angle of the head (Fig. 3F) and the lateral angle of divergence of the mandibular lips increased to 48°. At this point, the floor of the oral cavity was stretched between the mandibles but there was no evidence of a distension of the ventral pouch lateral to the mandibles. Fig. 3G-I shows the closing of the mouth both by elevation and adduction of the lower jaw and the downwards movement of the rostrum. The ventral pouch just behind the symphysis was distinctly swollen lateral to the left mandible and the vertically oriented grooves curved around the distended throat (Fig. 3I-K). The mandibles remained partially abducted from the rostrum (Fig. 3I-L), providing a clear view of the baleen plates and creating a groove (orolabial sulcus) of the open vestibulum oris lateral to the baleen plates and at the gape (Fig. 3I-L). Thus a partial

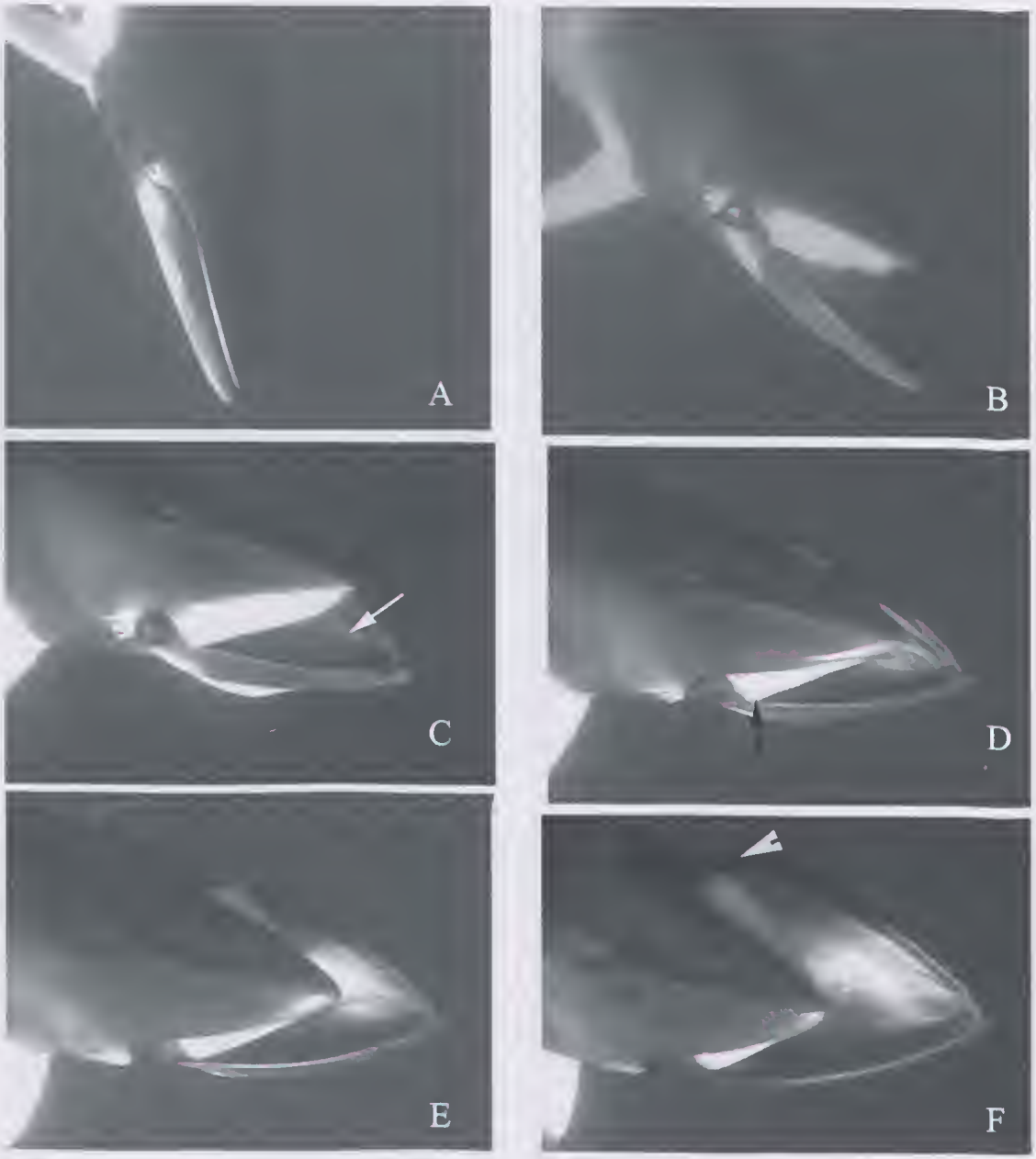



FIG. 3. Inter-mandibular gulp IM4. The mouth is just starting to open in A; baleen plates are visible in B, while the lip of the mandible appears to be oriented vertically. In C the mandible continues to drop and the rostrum is raised; the baleen plates are almost entirely exposed, revealing the dark plates at the posterior end of the baleen series; the lips of the mandibles are still vertical and form a sharp angle at the mandibular symphysis, thus showing minimal signs of alpha rotation and no lateral rotation. The curved structure just behind the mandibular symphysis (arrow) is the fibrocartilage skeleton of the ventral pouch. In D, the lips of the mandibles are still vertical and the mandibles still remain medial to the eye, again showing minimal signs of rotation. The white baleen plates are clearly visible and can be seen to protrude either side of the upper jaw, especially the longest plates which occur just before the angle of the gape (arrow). In E, the rostrum is raised, while the angle of lateral divergence of the mandibles has increased and the profile becomes increasingly bowed outwards, reaching a maximum in F. In F, the lip of the mandible (broad arrow) is just lateral to the profile of the head, so that a distinct gutter is formed lateral to, as well as just behind the baleen plate series.

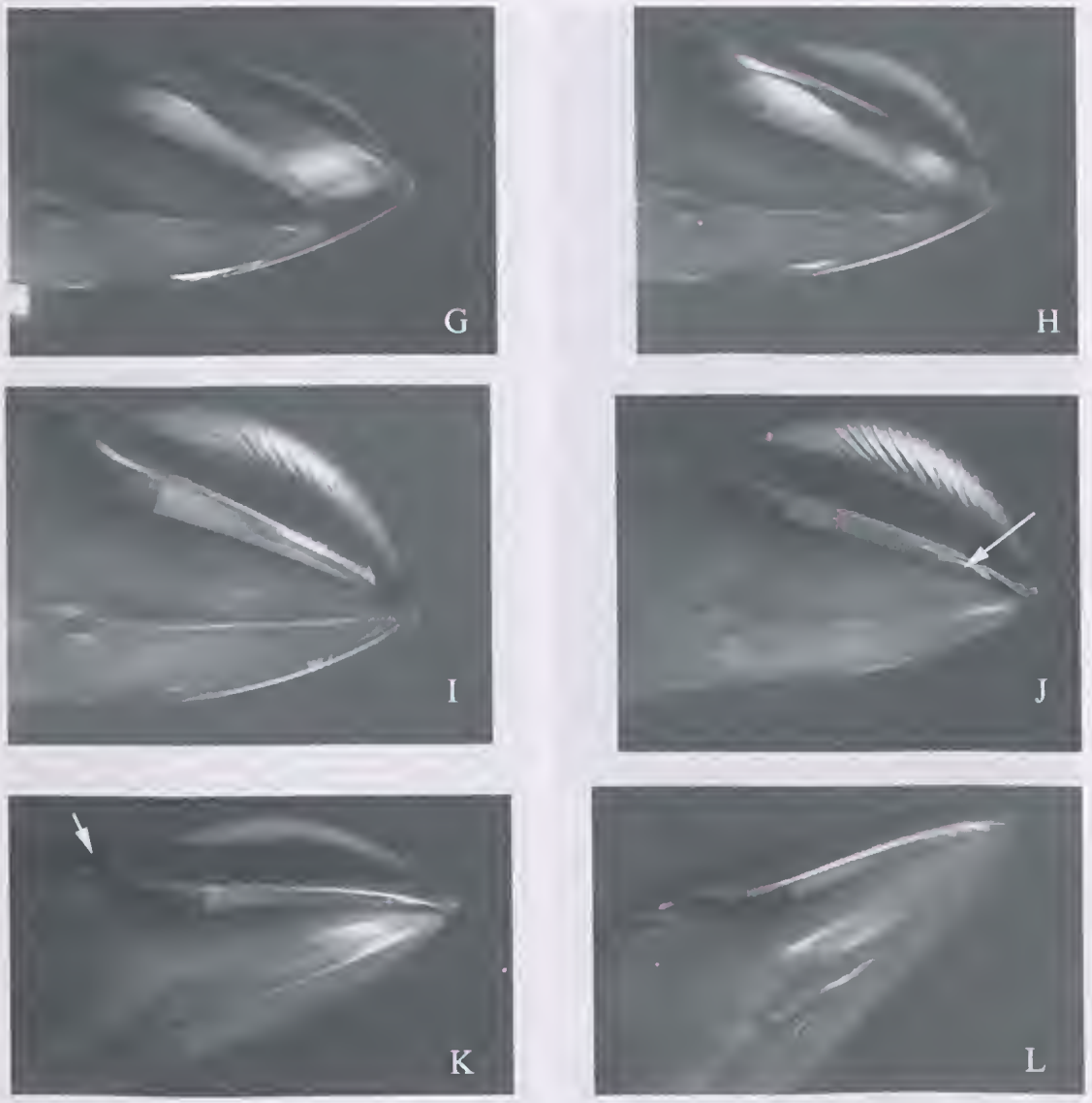



FIG. 3 (continued). This is consistent with full axial rotation of the mandible and also may indicate limited lateral (omega) rotation. A series of concentric wrinkles in the floor of the ventral pouch (thin arrow) denotes the anterior limit of the tongue. There is no sign of lateral distension of the pouch beyond the mandibles, although the floor of the oral cavity has been stretched outwards as the mandibles diverge. G, first signs of lateral swelling or distension of the ventral pouch are indicated as the white of the throat is seen beyond the left mandible. Note the upper and lower jaws are already closing. The lower jaw is still laterally displaced creating the gutter near the angle of the gape. H, swelling of the ventral pouch continues while the mouth closes; the gutter at the angle of the gape would allow displacement of water posterior to the baleen plates; the jaws have not been brought together closely enough for water to be filtered through the baleen plates. I, The mandibles are adducted towards the upper jaw, they already extend beyond the tip of the upper jaw. J, the ventral pouch reaches maximum expansion. The apparent whitish diffuse discolouration of the mandible (arrow) actually indicates fringes of baleen trapped as the lower jaws are brought back into position. K, L, mandibles are maintained at an angle to form a gutter just lateral to the baleen plates and opening as a posterior slit (K, arrow) through which water can exit to the rear. There is a steady expulsion of water, indicated by the deflation of the ventral pouch. Note the narrow vertical angle between the upper and lower jaws, leaving only a small portion of the base of the baleen plate series exposed- much of the water would exit along the gutter formed by the mandibles.

FIG. 4. A, Inter-mandibular pouch distension in gulp IM3. Expansion of the ventral pouch reaches its maximum about level with the eye; the body in the shoulder region remains unexpanded. B, Full ventral pouch gulp (VP1).The dark throat patch is obvious; also note that most of the pouch expansion occurs posterior to the inter-mandibular area.

alpha rotation of the mandible was maintained (compare Figs 1 and 3), providing a channel along which water could exit posteriorly after passing through the baleen plate series. The tongue was not seen at any stage of the opening of the jaw; concentric wrinkles just visible in the mid intermandibular region at the point of maximum opening of the mouth (Fig. 3F, arrow) probably indicate the anterior margin of the tongue which would have been in the posterior part of the throat at that stage.

Gulps IM1 (Fig. 6) and IM2 (Fig. 7A), as well as VP1 (Fig. 8A) also showed that the lower jaw may drop while still maintaining a low angle of lateral divergence of the mandibles –i.e. with only minimal evidence of alpha and no apparent omega rotation. It was only when the jaw was depressed to about its maximum extent that there was a divergence of the mandibles, involving both alpha and omega rotation (see below).

Gulp IM3 showed a small distension of the ventral pouch as the jaw dropped, however it was only as the lower jaw was being closed that there was a distinct bulging of the ventral pouch (Fig. 4A) and substantial alpha rotation, as well as some lateral rotation (as indicated by the stretched frontomandibular stay and rotated lip of the lower jaw).

Gulps IM1 and IM3 included an oblique latero-posterior view of the whale as it swam away at the end of the gulp sequence. Gulp IM3 (Fig. 5) shows clearly that the mandible was held away from the upper jaw, not only leaving the baleen plates exposed but also forming a gutter between the baleen plates and the mandible which was open as a posterior slit at the gape, as also seen in IM4 (Fig. 3). The greatest abduction occurred at the rear of the channel, so that water could escape as the jaws were closing (Fig. 3H,I).

*Omega rotation*. Gulp IM2 (Fig. 7A) provided the best view of the angle of the mandibles at full divergence during a gulp. The posterior lip of the mandible was separated by a wide space from the external angle of the head, overlying the supraorbital process of the skull (Fig. 7A). This is a direct confirmation of lateral or omega rotation, spreading the mandibles widely to increase capture area. The angle of the mandibles (52° in oblique view, thus an underestimate) exceeded that associated with full alpha rotation in IM4 (see above). Although the lips of the mandibles formed an almost straight line, the anterior part of the frontomandibular stay could be seen diverging laterally from the gape to insert on the medial body of the mandible at the point of maximum curvature (IM1: Fig. 6, IM2: Fig. 7A). Thus the opening into the ventral pouch was an elongated ellipse, which was smaller in area than would be calculated from measuring the angle of the lips of the diverging lower jaws.

Gulp IM1 was videotaped from a more lateral aspect and thus it is difficult to assess the outward movement of the mandibles. However there was a wide separation of the lip of the mandible from the upper jaw and the frontomandibular stay could be seen stretched at the angle of the jaw (Fig. 6A). The extent of separation of the jaws would not occur solely through axial or alpha rotation and thus confirms omega rotation.

The temporal ridge formed by the frontomandibular stay may limit the extent of

separation of the jaws; on stranded specimens it can be seen as a thick column, strongly folded or pleated, which indicates the potential for considerable extension (e.g. figure of Antarctic minke whale *B. bonaerensis* in Baker, 1990: 10).

*Delta rotation.* Delta rotation involved not only depression of the lower jaw but also raising of the head and rostrum. This was particularly evident in inter-mandibular gulps IM1 (Fig. 6), IM2 (Fig. 7A) and IM4 (raising of rostrum seen in Fig. 3), although limited raising of the head was seen in other gulps, including VP1 (Fig. 8). Maximum vertical separation of the mandibles and upper jaw (delta rotation) occurred in sequences IM1 and IM2, with angles of 60-70°. This was due almost equally to raising the rostrum and dropping the mandibles. Other inter-mandibular gulps and the full ventral pouch gulp (VP1) had a maximum opening of about 40° which fully distended the ventral pouch (Fig. 8).

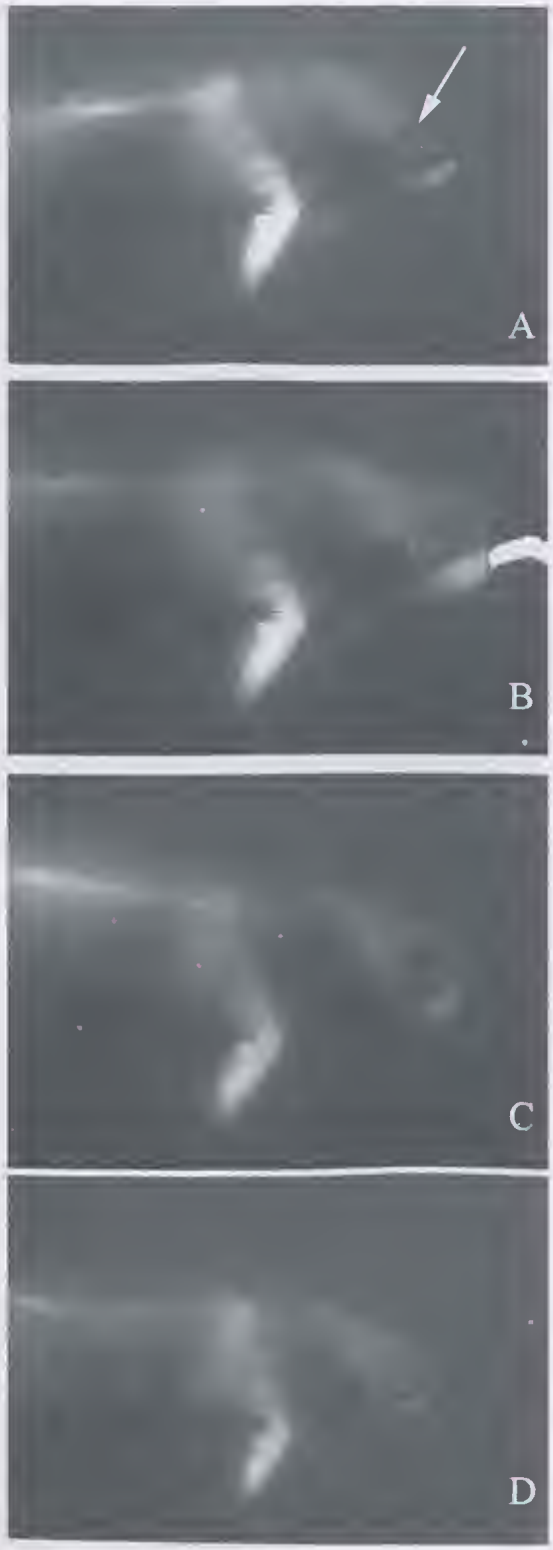
Once the rostrum was raised, there would be an upwards force on the palate as the whale moved forward, keeping the rostrum elevated. This may be partially compensated for by the forward rotation of the flippers (IM1, Fig. 6A,B). However, movement of the head was actively controlled and not simply a response to upward force of the water. In gulp IM4, for instance, the head was raised, briefly lowered, then raised further before being brought back towards the lower jaw.

At the end of a gulp, the head was brought down to close the mouth. In gulps IM1 and VP1, where the sequence of events could be followed, the head was brought down only after the mandibles had returned to a horizontal position (VP1, Fig. 8). Timing of closure needs to be precise. Fig. 3D of gulp IM4 shows how far beyond the rostrum the baleen plates extended, especially the longest plates that occur about two-thirds of the way back in the series. As has been noted before (Lillie, 1915; Pivorunas, 1977), curvature of the mandible is needed to swing around these extended baleen plates. However, by the time the mouth was nearly closed, being open only at the anterior end, the mandibles had returned almost to the position they occupied when the whale was swimming normally (Fig. 3I, J). On two occasions we have seen and photographed the anterior-most baleen plates being trapped as the mandibles closed onto the rostrum (Fig. 3J).

ROLE OF THE FIBROCARTILAGE SKELETON. In all the inter-mandibular gulps, there was an initial distension or ballooning of the ventral pouch in the mental area just behind the symphysis (e.g. IM1, Fig. 6B). This could be followed by an expansion of the rest of the inter-mandibular area, but the mental swelling remained visible, defined by a ridge-like structure running posteriorly (IM1, Fig 6; VP1, Fig. 8), around which the vertically oriented grooves curved. This ridge corresponds in position to one of the bifurcating branches of the fibrocartilage skeleton. In the ventral pouch gulp (VP1), initial bulging of the ventral pouch occurred more posteriorly (Fig. 8B), but this was immediately followed by a distension of the pouch in the mental region (Fig. 8C,D), just as in the inter-mandibular gulps. The vertically oriented grooves curved over a ridge-like structure as in the inter-mandibular gulps (Fig. 8D); this again is consistent with the position and structure of the fibrocartilage skeleton. In sequence VP1, as well as two other ventral pouch gulps photographed, maximum distension of the pouch occurred below the nape region, between the mouth and flipper, so that the ventral profile was of a parabola or smooth curve (Fig. 8F-K).

In gulp VP1, expulsion of water occurred in two stages. Initially the ventral pouch from the anterior ballooning of the mental region to its posterior insertion just in front of the umblilicus contracted as a unit, maintaining the smooth curve of the ventral profile, so that there was a less perceptible difference between the anterior ballooning of the mental region and the rest of the ventral pouch (Fig. 8F-K). Subsequently, the bulge in the ventral profile was restricted to the inter-mandibular area. Water within the ventral pouch appeared to be squeezed smoothly from the thoracic region towards the throat or inter-mandibular area, from which the last of the water was expelled after bulging in the mental region. In neither this sequence, nor in a second sequence (not illustrated) showing a full ventral pouch gulp, was there any indication of a forward movement of water in the ventral pouch as would be expected if there was a bounce mechanism assisting the closure of the lower jaw.

At the completion of the inter-mandibular gulps, the extent of white visible on the throat decreased as water was expelled through the baleen plates. In gulps IM1 and especially IM3, this was subsequently followed by a bulge in the throat which traveled forward to the mental region just behind the mandibular symphysis where it formed a distinct bulge over the fibrocartilage skeleton (IM3, Fig. 5B). This bulge




then decreased in size (IM3, Fig. 5C, D), bringing the inter-mandibular region back to its normal streamlined profile. Our interpretation of this forward traveling bulge is that it represents the last portion of water expelled, possibly forced forward by the tongue returning to its normal, more anterior position.

VERTICAL ANGLE OF JAWS DURING EXPULSION OF WATER. In lateral view, there was a narrow vertical separation of upper and lower jaws, giving a delta rotation of approximately 2°-5°, which exposed the baleen plates to view (Figs 6D, 8K). Given the partial abduction of the lower jaw, a groove was formed outside the baleen plates into which water could be expelled (IM3, Fig. 5). The exposed portion of the baleen plates corresponded to the basal half of the plates. Thus, at least at the beginning of water expulsion, the area for egress of water (exposed baleen plates plus groove) was very much smaller than the surface area of the contracting ventral pouch.

LENGTH OF BALEEN PLATES. In dwarf minke whales, the baleen plates progressively increase in length to a maximum at about two-thirds of the way back, after which there is a sharp decrease in length. This profile is not only evident in lateral view but also dorsal view (IM4, Fig. 3D) where the longest plates extended furthest beyond the lateral borders of the rostrum. Gulp IM4 (Fig. 3H, I) shows the opening of the vestibulum oris at the gape. The longest plates are at the gape, with the forward extension of the frontomandibular stay crossing just lateral to the tips of the plates. These long plates would thus be the primary ones trapping food as water was expelled between the baleen plates into the posterior opening of the gutter at the gape.

## DISCUSSION

The gulps which we filmed were not associated with feeding, as we never saw any food in the water. The two main types of gulps we documented (inter-mandibular, full ventral

FIG. 5. End of gulp IM3, showing beginning (A) of expansion of the ventral pouch in the mental region, which reaches its fullest extent in B and then begins to contract again in C and D. B shows the swelling of the mental region over the area covered by the fibrocartilage skeleton. Note in each image that the mandible is held out from the baleen plates through partial alpha rotation, creating a gutter (arrowed in A) and posterior slit for exit of the water.

pouch), may have different functions. The inter-mandibular gulps may be used as a display to swimmers (Birtles et al., 2002) and to other whales (unpublished observations). They showed a greater variability in duration than did the full ventral pouch gulps (Table 1). Whether or not these inter-mandibular gulps are also used in feeding, they do indicate the mechanics of oral cavity distension. The full ventral pouch gulps, in their duration and characteristics, are comparable to the lunge feeding seen in other rorquals (see comparisons below).

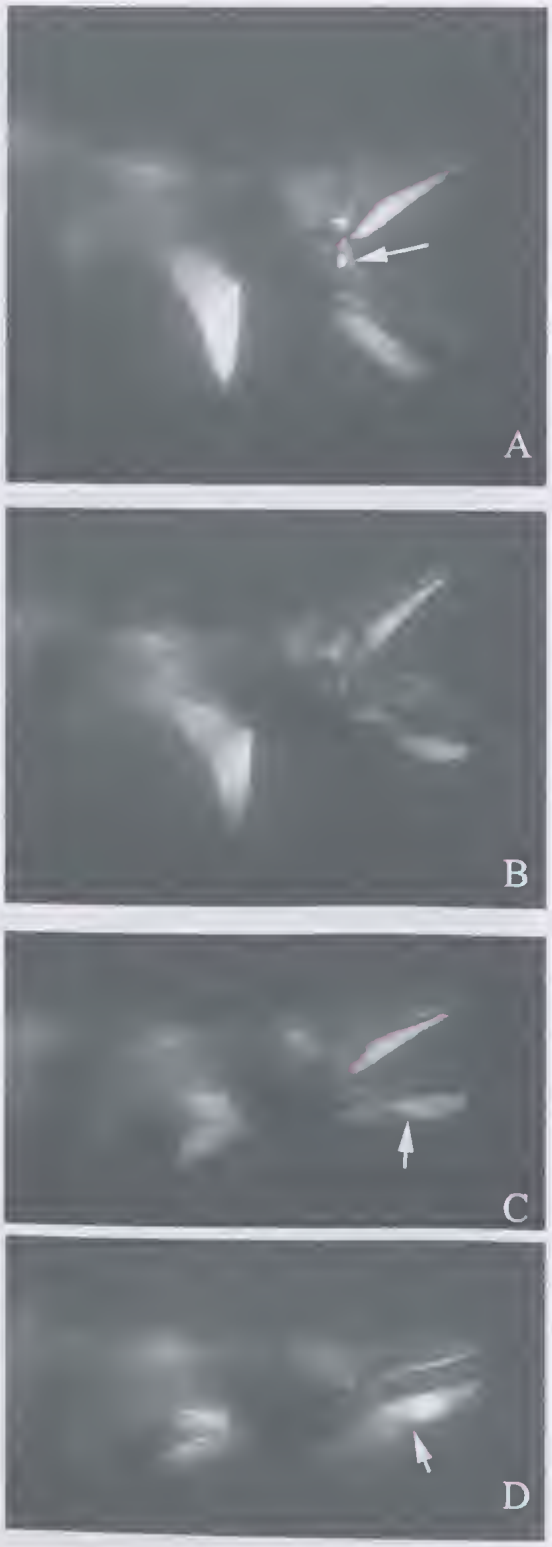
CHARACTERISTICS OF GULPS. The extent of pouch filling did not relate to the time the mouth was open; in inter-mandibular gulps IM1 and IM2 the maximum filling of the pouch took 5.5-5.7 seconds, while the full ventral pouch gulp VP1 lasted only 3.0 seconds. In all gulps which we observed underwater, the whale was progressing forward (pers. obs.; video of IM1). Thus whether only the inter-mandibular area or the whole pouch filled could be linked neither to the length of time that the mouth was open nor the occurrence of forward progression. Since the videographer followed the whale with the camera in open water, we could not to assess the speed that the whale was traveling. Thus we can not check the relationship between the time taken to fill the ventral pouch and swimming speed.

Full alpha and omega rotation occurred in gulp IM2 but did not result in full expansion of the ventral pouch even in the inter-mandibular area; this contrasted with another sequence which had similar alpha and omega rotation but a fuller ventral pouch gulp. This difference suggests that expansion of the oral lining may not be entirely passive but under the control of the whale. Possible control mechanisms are discussed below.

In the sequences presented here, the whale could change the orientation of the head and travel of the body (either vertically or laterally) and thus the angle at which the water entered the mouth. However, in both IM1 and VP1, the whale was diving from the surface when the gulp began, so type of gulp was not directly related to the orientation of the whale as it traveled forward.

Initially, we thought that the rapid downward swing of the head could act as a lid on the still open ventral pouch but this downward sweep of the upper jaw occurred only after the mandibles had returned to a horizontal position and thus the opening of the ventral pouch was normal to the water flow (i.e., more water would not flow in).

We do not rule out the role of behavioural factors (e.g. length of time that the mouth is open, speed of travel, angle of travel of the body) in determining the extent to which the pouch fills; such factors could be particularly important in IM3 and IM4, which lasted for only 2.0 and 2.6 seconds respectively. However it does not explain the difference in filling of the pouch between IM1 and IM2 on the one hand and VP1 on the other. We suggest that there may be an anatomical basis as well. The ventral panniculus muscle extends for the whole length of the ventral pouch but the anterior and posterior portions of the muscles have different innervation: the facial nerve in the inter-mandibular area and the lateral thoracic nerve posteriorly (Schulte, 1916, based on observation of sei whale). In the humpback whale, Lillie (1915) illustrated two different sets of transverse muscles in the inter-mandibular area and thoracic area respectively. It thus seems possible that in an inter-mandibular gulp, the anterior inter-mandibular portion of the panniculus, as well as other transverse muscles such as the mylohyoid, relax while the posterior panniculus and thoracic muscles remain contracted. This would limit the backward movement of the tongue and the ability of the cavum ventrale to open up and receive the tongue. Relaxation of the posterior panniculus and transverse muscles in the thoracic region, as well as the inter-mandibular muscles, would allow full ventral pouch distension. One of the problems in testing this speculation is the poor documentation of baleen whale myology. Pivorunas (1977) and Lambertsen (1983) provided clear and well-illustrated re-descriptions of the inter-mandibular muscles. However, our Figs 4 and 8, in particular, show how great an area posterior to the inter-mandibular region is involved in a full distension of the ventral pouch. We are unaware of any detailed study on muscles which overly this posterior region of the ventral pouch. The classic anatomical study on a common minke whale by Carte & Macalister (1868) was based on a single individual which had been dead for nearly two weeks before it was made available for dissection; similar constraints of limited sample size and extensive post-mortem times affected the description of a blue whale by Turner (1870), fin whale by Delage (1885) and humpback whale (Struthers, 1888). Lillie (1915) had access to fresh material. His observations, such as on axial rotation of the mandible, were astute and have been well supported by subsequent research, however his illustrations




were diagrammatic and his anatomical descriptions were very limited. The much quoted monograph by Schulte (1916), to which we refer above, was based on a sei whale foetus only 36 cm long. Thus there is a need for new, detailed anatomical descriptions of the whole ventral pouch before our suggestion of anatomical control of gulp feeding can be tested.

As pointed out by Brodie (2001) and Lambertsen & Hintz (2004), greatest resistance may occur at the beginning of opening of the jaws through frictional effects of the mandibles passing over the outwardly directed baleen plates and, perhaps more so, hydrostatic sealing of the mouth. Our observations of gulp IM4 show that the jaw is almost vertical as it drops initially so there would be some frictional resistance. In two of the sequences, where we saw what happened leading up to the gulp, there was a brief, narrow opening of the mouth ("preliminary" gulp). This may allow water into the oral cavity, breaking any hydrostatic seal; it may also clean the baleen plates.

JAW ROTATION: *delta rotation*. Images of feeding rorquals (Pivorunas, 1979; Lambertsen, 1983; Brodie, 1993; Berta & Sumich, 1999; Werth, 2000; Croll & Tershey, 2002; Heithaus & Dill, 2002; Hewitt & Lipsky, 2002; Bouetel, 2005) show a horizontal rostrum with the mandibles depressed at or almost at a right angle.

In our observations of dwarf minke whales, the opening of the mouth varied from about 40°-70°,

FIG. 6. Gulp IM1. A, As much of the delta rotation comes from raising of the upper jaw as depression of the lower jaw. The outward deflection of the lip of the lower jaw and the ventrally oriented, stretching frontomandibular stay of the jaw (arrow), indicates axial rotation of the lower jaw and, through the deflection of the lower lip and extension of the frontomandibular stay, probable partial omega rotation. B, the lower jaw is closing, while the upper jaw and head remain raised. In A and B, the swelling is predominantly in the mental region. C, the lower jaw has returned to a horizontal position while the upper jaw is still being brought down to its normal position; the bulge over the fibroeartilage skeleton (arrow) is clearly seen. D, there is an indication that water in the ventral pouch is being redistributed posteriorly, with distension of the ventral pouch behind the mental region. Note the position of the flippers, which are brought forward in A and B, then return to their more medial, more posteriorly oriented position (C, D) which is normal when swimming.

with the widest opening associated with inter-mandibular gulps. In the widest openings we observed, the rostrum was raised almost as much as the mandibles were depressed, presenting quite a different profile to that illustrated in the literature. Although we use the term "delta rotation" for such an opening of the mouth, the depression of the mandible itself was less than about 40° and thus much less than the delta rotation of 90° for the mandible which has been generally suggested in the literature quoted above.

Rapid (3 second) and full expansion of the ventral pouch could occur in non lunge-feeding dwarf minke whales with an opening of only 40° (Table 1:VP1). But is this also the case in feeding whales? Gaskin (1976) indicated that fin whales feeding at the surface on euphausiids opened their mouth to an angle of "45° or more". Watkins & Schevill (1979), observing the same species feeding on fishes, noted maximum jaw openings estimated as 10°-20° and 30°, the latter when the jaw was closed more quickly. Further, feeding gulps did not always appear to be to capacity; Watkins & Schevill (1979) noted variable distension in feeding fin whales and noted that an individual might make a series of three to four gulps while feeding on fish. Mouth openings of at least 80° occur in video sequences of feeding Bryde's whales (BBC: *Wild Australasia*), however this appeared to include raising the upper jaw as well as depressing the lower jaw. In blue whales observed feeding off southern Australia, gape varied from about 60° to 80°- 85°, with the more usual gape estimated as about 70° (P. Gill, pers. comm.). Gill further noted that it "does seem that the wider [the blue whales] gape, the more the rostrum lifts back, as the mandible drops down". Such records suggest that the images showing a right angle depression of the mandibles may represent an extreme case rather than the general condition in feeding rorquals. The ventral pouch structure must be able to withstand the maximum stress, such as would occur with an opening of 90°, and thus such angles are appropriate to consider in discussions on mechanics such as Lambertsen et al. (1995). However, a discussion of evolution of gulp feeding needs to consider the more general case, which appears regularly to be a mandibular delta rotation of <70°, perhaps considerably less.

Lambertsen & Hintz (2000) discussed the mechanisms for preventing water in the ventral pouch from bouncing forward and out of the still widely open oral cavity; they alluded to such mechanisms as critical in developing a "rorqual adaptive zone". Such a bounce mechanism seems very likely in a configuration of the ventral pouch such as shown in Pivorunas (1979) and elsewhere in the literature. It might also occur in the inter-mandibular gulps we document, if the whale is travelling quickly. However in full ventral pouch gulps, such as VP1, the lower jaw was already starting to close before maximum expansion of the ventral pouch occurred. This also happens in feeding whales, based on images of lunge feeding Bryde's whales (e.g. BBC: *Wild Australasia*; images from Peter Constable). Water would thus still be flowing into the pouch as the mandibles were returning to their normal position. With water still being accommodated in the posterior portion of the ventral pouch as the mouth closes, water would not build up in the inter-mandibular area or bounce forward out of the still open oral cavity. With only the resistance of the mandibles, the lower jaw could return to the horizontal position relatively rapidly. This would be especially true in cases with a delta rotation of 40° or less for the mandibles, in which case there is less distance for the mandibles to be elevated before they are normal to the direction of travel and thus impede the inflow of more water. Minke whales (as well as sei whales) have a relatively short ventral pouch, with ventral grooves occupying about 47% of the body length (Nemoto, 1959). In blue, fin, Bryde's and humpback whales, the ventral pouch is relatively longer, with ventral grooves occupying 58, 55, 58 & 58% of the body length respectively (Nemoto, 1959). The additional 11% in length of ventral pouch would translate into a significant increase in capacity; this can be seen in the almost cylindrical profiles of the full ventral pouch in blue whales (e.g. Grace, 1996; Clapham, 1997) rather than the semi-circular form of the ventral pouch shown in diagrams of feeding (Pivorunas, 1979 and others listed above). Thus the potential for rapid closure of the lower jaw while water is still filling the ventral pouch is even greater in species such as blue and fin whales, than has been demonstrated here for minke whales. This closing of the jaws while water is still filling the ventral pouch is central to the development of lunge feeding and the "rorqual adaptive zone".

We saw no evidence of the bounce phenomenon after jaw elevation and adduction in the admittedly limited number of full ventral pouch gulps we have recorded. The bounce phenomenon might occur in true lunge feeding, however. One sequence of lunge feeding Bryde's

FIG. 7. A, Gulp IM2. Note the extensive lateral divergence of the mandibles, stretching the floor of the oral cavity. The upper arrow indicates the most lateral extension of the supra-orbital process of the head, at the base of the rostrum, while the lower arrow indicates the position of the lower lip. The wide gap between the arrows is greater than would be expected from axial rotation alone (Fig. 3) and indicates a lateral displacement of the lower jaw consistent with omega rotation. The angle of the mandibles exceeds that which would be consistent with full alpha rotation, as shown by the curvature of the upper mandible shown in B. B, Mandibles of a 7.1 m dwarf minke whale (QM JM3861) which are rotated laterally to different degrees. Upper mandible better illustrates the extensive lateral curvature.

whales (BBC: *Wild Australasia*) showed what appeared to be a forward movement of the water in the ventral pouch; it occurred well after the mouth had closed. It may have assisted in expulsion of water through the baleen plates but was only seen in one of the gulps. The control of a bounce phenomenon may thus be largely behavioural, i.e. closing the mouth before the ventral pouch has fully expanded to avoid a bow wave effect and rapidly closing the mouth to contain any movement of water later in the gulp. A further behavioural control would be in the timing of opening the jaws. This should occur only when the whale moves into the concentrated prey, in order to maximize the density of food contained in the water pouring into the expanding ventral pouch. Such behavioural controls are essential to fully exploit any morphological specializations ("rorqual adaptive zone") for the capture of highly mobile prey.

*Role of cranial movement in delta rotation.* The mobility of the head and upper jaw was evident, especially in inter-mandibular gulps. Gulps IM1 and IM4 showed particularly well how raising the head and upper jaw could contribute to the extent of gape during a gulp. That this may also occur in full ventral pouch gulps of feeding whales is shown by the accounts and illustrations of elevated head and upper jaw in feeding fin whales (Gaskin, 1976, fig. 18), images of lunge feeding Bryde's whales (BBC: *Wild Australasia*) and the observations on blue whales by Gill, quoted above. Schulte (1916) noted the semispinalis capitis was the largest of the dorsal neck muscles; it has a "broad and deep" insertion on the supraoccipital. He also described "a great muscle complex" originating from the ribs and anterior spine and inserting on the base of the skull. Such muscles would be well placed for the respective elevation and depression of the head and upper jaw.

*Alpha rotation.* During normal swimming, the lower jaw is tightly adducted against the upper jaw and initially in the gulp only limited alpha rotation was seen. The lower jaws would thus have dragged over the baleen plates, with some frictional resistance (Brodie, 2001). At this stage, with only limited inflow of water, there would be no torque on the mandibles from filling of the ventral pouch (Lambertsen et al., 1995). In gulp IM4, as well as IM3, significant distension of the pouch in the mental region was seen only after the upper jaw was actively raised, at which point a clear lateral curvature of the mandibles was seen in IM4 associated with alpha rotation. The angle of divergence of the mandibles (Fig. 3F) and the position of the posterior portion of the lower jaw, level with or only slightly external to the frontal surface of the head, suggest that the movement of the mandible was predominantly, if not exclusively, due to rotation around its axis- i.e. the alpha rotation of Lambertsen et al. (1995). This would appear to be the maximum extent of alpha rotation as the curvature of the lower jaw in the images corresponded to the curvature of the mandible when it is allowed to fully rotate outwards (Fig. 7B ). This was a particularly fast gulp (about 2.6 seconds) and it may not have been long enough to allow fuller expansion of the

ventral pouch leading to omega as well as alpha rotation. However, it is clear from this gulp and others (IM2, Fig. 7A; VP1, Fig. 8) that initial opening of the mouth may occur with only partial alpha rotation and no apparent omega rotation. This is also supported by video of a lunge feeding Bryde's whale (*Blue Planet: Open Seas;* identified as a sei whale) in which the lower jaw dropped with a dorsoventral curvature of the lower jaw, and thus mandible. This dorsoventral curvature occurs when the mandible is adducted against the rostrum (Tomilin, 1967, fig. 38). For the dorsoventral curvature to remain visible in lateral view, at most only partial alpha rotation must have occurred; moreover there was an inpocketing of the mental region which would not occur if water was pouring in at that stage. Lambertsen et al. (1995, table 2), in their model of passive filling envisioned almost immediate and complete alpha and omega rotation, with full alpha rotation from 45° to 0° as delta rotation increased to only 10°. Our sequence of gulp IM4 shows that a partial alpha rotation could occur at the beginning of the gulp sequence without any omega rotation, and that full alpha and omega rotation did appear to occur simultaneously but only when the jaw had reached full delta rotation (i.e. much greater than the 10° of Lambertsen et al., 1995). This sequence does not confirm the timing of mandible rotations postulated by Lambertsen et al. (1995).

The mandibles remained partially abducted at the end of gulps, forming a gutter (orolabial sulcus) leading to posterior vertical slit at the end of the open vestibulum oris (Fig. 3G-L). The widest expansion occurred at the rear of the channel, so that water could escape as the jaws were being closed (Fig. 3G, H); thus the term "spillwater groove" used by Struthers (1888) for this posterior opening is quite appropriate. That this is an important channel for the egress of water forced between the baleen plates is confirmed by underwater video of feeding Bryde's whales (*Blue Planet: Open Ocean*) in which contents of the ventral pouch could be seen streaming backwards not only from the anterior baleen plates but in a clear stream from the posterior opening of the groove formed by the partially abducted lip of the mandible.

The formation of the groove could occur only through a partial and actively controlled alpha rotation of the mandible and lower jaw. Lambertsen & Hintz (2004) noted the potential role of the superficial masseter muscle in tightly adducting the lower to the upper jaw. Relaxation of the superficial masseter may be involved in the partial alpha rotation which we have documented as a regular feature of the gulp sequence in both inter-mandibular and full ventral pouch expansion. The major impediment to this process would be if there is a hydrostatic seal between the mandible and upper jaw. There is no question that the mandible and baleen plates are normally tightly opposed, to the extent that imprints of the lateral edges of the baleen plates are left on the medial surface of the mandible. However whether this is due to a hydrostatic seal or due to muscular contraction of ventral pouch , especially through longitudinal muscles (see below) can not be decided on available evidence. Lambertsen et al. (1995, fig. 12a) and Lambertsen & Hintz (2004, figs 2e, 3), show that the adducted mandible is rotated so that the lateral face of the neck of the mandible and the lateral face of the coronoid process are dorsal, while the medial face is ventrad. This would also follow from the statement in Lambertsen & Hintz (2004) that the lateral surface of the coronoid process just below its crest would provide the primary articulating surface with the maxilla, as well as the 45° angle of the mandibles in medial position in Lambersten et al. (1995, fig. 12a). With such an orientation, the contraction of the pterygoid muscle, inserting on the medial surface of the angle of the mandible, would serve to rotate the mandible outwards. This may provide the initial power that overcomes frictional resistance and/or breaks the seal and allows the lower jaw to rotate outwards sufficient to allow inflow of water. Only a small deviation in the angle of the jaw would be needed. At the end of the gulp, there is a fine control of the angle of the lower jaw to form a groove where water exits. At this stage the lateral surface of the mandible would again be more dorsally directed and there could be an antagonistic action of the superficial masseter, rotating the lower jaw inwards and the combination of water mass and relaxation of the internal pterygoid rotating it outwards. The tendon of the contracted superficial masseter might act as a guide or cam mechanism in the rotation of the mandible at this stage (Lambertsen & Hintz, 2004).

Evidence for cam articulation is based on computer models and is still circumstantial. The partial alpha rotation documented here in minke whales is not evidence of the cam articulation. Equal degrees of alpha rotation are evident in dead right (Slijper, 1962; True, 1904) and bowhead (Lambertsen et al., 2005) whales, as

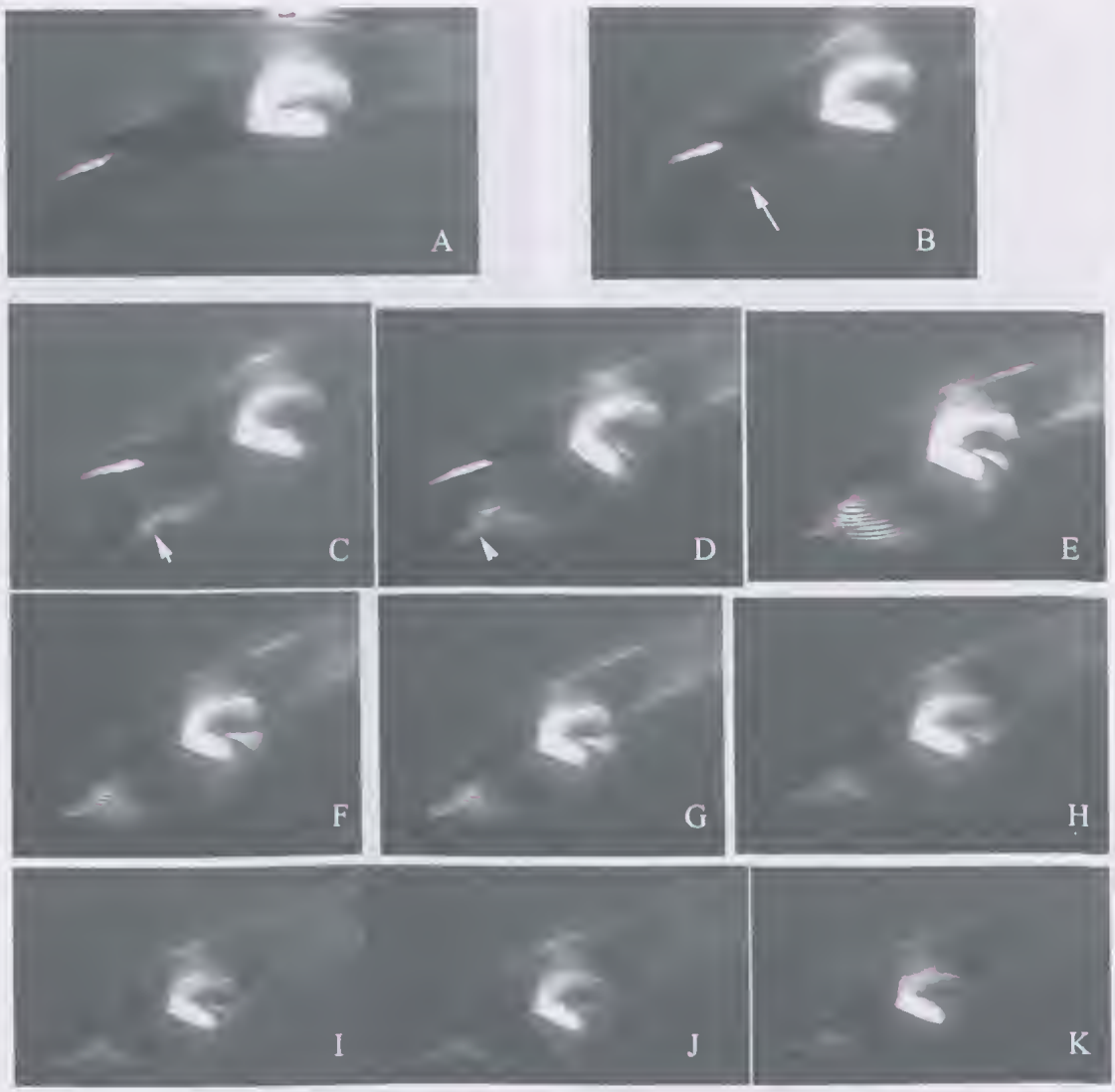



FIG. 8. Full ventral pouch gulp VP1. A, the narrow angle of lateral divergence of the mandibles as the jaw is lowered, indicates little alpha and no omega rotation. In B, the filling of the ventral pouch starts behind the mental region (arrow). C, the ventral pouch distends through continuation of the posterior swelling first seen in B, as well as expansion of the mental region overlying the fibrocartilage skeleton. The vertically oriented grooves are curved around the backwardly directed left arm of the fibrocartilage skeleton (arrow) and the ventral pouch seems to be divided into two discrete areas. The two areas remain distinct in 8Dd and 8Ec, as the ventral pouch reaches maximum expansion. Note also the smooth curvature of the ventral pouch as it is fully distended; the water may still be expanding the pouch as it is re-distributed posteriorly, but the mouth is closed at the point of maximum distension of the ventral pouch. F-K. This series of images shows expulsion of water. Note the small vertical angle between the upper and lower jaw, limiting exposure to the base of the baleen plates. Note also that the ventral profile of the pouch retains the smooth curve seen at the point of maximum expansion. There is thus no indication of a forward movement of water or "bounce phenomenon" envisioned in some models of water expulsion in rorquals.

well as video (*The Lost Whales*, New Zealand Natural History Unit) and studies of living balaenids (Werth, 2004a). Partial alpha rotation of the lower jaw is also evident in photographs of stranded pygmy right whales (Gaskin, 1972; Baker, 1990) and gray whales (Leatherwood et al., 1988). Balaenids, pygmy right whales and gray whales all appear to lack the skull structure needed for the cam articulation proposed to occur in rorquals (Lambertsen & Hintz, 2004).

A major difference between rorquals and other baleen whales is in the head profile (Lambertsen & Hintz, 2004; Lambertsen, 2005). In particular they suggested that the marked asymmetry between upper and lower jaws in rorquals would generate significant negative lift on the lower jaw that would need to be counteracted by a mechanism such as the cam articulation to prevent the lower jaw from opening, especially when the whale is swimming quickly. There appears, however, to be considerable variation in form of the upper jaw (as opposed to rostrum of the skull) in rorquals. While it is broad and flat in blue whales, it is highly sloped along the median ridge in minke whales (Fig. 1; see also Williamson (1972), pl. 3a,b). The profile of the head in minke whales, seen in lateral or anterior view, approximates a forwardly directed cone, with much less asymmetry between the upper and lower jaw than envisioned by Lambertsen & Hintz (2004). This would minimize the extent of negative lift they envision and thus the need for a mechanism such as the cam articulation. Moreover, the orientation of the head of a rorqual whale to the direction of water flow may vary considerably as it swims forward, especially in a highly manoeuvrable species such as minke whale. In dwarf minke whales, the head may pitch routinely as the whale swims (pers. obs.), presenting a continuously changing profile for water flow over the body. This creates a complex pattern of water flow which may not correspond to the simple hydraulic models for lift considered in discussions of gulp feeding and development of a "rorqual adaptive zone".

*Omega rotation*. Our underwater observations confirmed the lateral displacement of mandibles, or the omega rotation of Lambertsen et al. (1995). Gulp IM1 shows that the separation of the lower jaw may not be only lateral but also ventrad.

In gulp IM2 (Fig. 7A), the antero-lateral oblique orientation of the fronto-mandibular stay can be seen - this stay not only limits lateral displacement of the mandibles but also defines the postero-lateral boundary of the opening into the oral cavity which is smaller than that which would be assumed based on lateral displacement of the mandibular lips. The lips of the mandible continue outwards, exposing a broad floor of the open vestibulum oris. The extent to which the vestibulum oris can expand, as well as the fronto-mandibular stay, may ultimately limit the lateral travel of the mandibles. Pivorunas (1977), in a dissection of *B. acutorostrata*, noted an intramuscular cleft, similar to the cavum ventrale, associated with the posterior face of the mandible. He suggested this could "aid the ventral pouch musculature in depressing the floor of the vestibulum oris that is located immediately dorsal to the mandibular furrows...". This might also allow a greater expansion of the vestibulum oris, accommodating the lateral movement of the mandibles.

Lambertsen et al. (1995) noted that as the lower jaws of humpback whales bowed out to maximum extent, the anterior tip of the lower jaw has to become displaced posteriorly to behind the rostrum; they illustrated the point (Lambertsen et al., 1995, fig. 8) with a lunge feeding humpback whale at the surface, which they used as evidence of omega rotation. While not disputing this as evidence of omega rotation, we note that this may be a feature peculiar to humpback whales, which have a particularly narrow rostrum for a rorqual and mandibles which are strongly curved laterally. In minke whales, by the time the upper and lower jaws were brought together, the mandibles had returned almost to their medial positions, to the extent that the anteriormost baleen plates could be trapped by the closing lower jaw. The tip of the lower jaw appeared to be anterior to the rostrum as in normal swimming (IM4, Fig. 31-L).

ROLE OF THE FIBROCARTILAGE SKELETON. Schulte (1916) suggested that deformation of the mental region would occur through the action of the mylohyoid and panniculus muscles on the fibrocartilage skeleton. In minke whales most of the spreading of the fibrocartilage skeleton occurred while the inter-mandibular area was expanded and thus the mylohyoid and panniculus muscles would be relaxed rather than contracted. Rather, we feel that the deformation of the mental region is a more passive process, driven by inflow of water at the beginning of the gulp. One line of evidence for this is that the fibrocartilage skeleton is clearly visible on carcasses, in which the muscles are flaccid (Pivorunas (1977) gave a long list of

FIG 9. Baleen flash in a dwarf minke whale, which has raised the upper jaw and baleen plate series out of water. The function of this behaviour is unknown (it may be associated with other behaviours such as bubble blasts or jaw clap and thus be a display) but it was not associated with feeding (i.e., no concentration of food was visible in the water). Similar behaviour has been described in sei whales, with the upper jaw and much of the baleen out of water; such behaviour has been attributed to feeding in sei whales but this may not always be the case.

published images; see also Clapham, 1997: 109). Pivorunas (1977) noted that the fibre structure of the fibrocartilage skeleton was not oriented in a single direction, as in a tendon, and thus referred to it as a "paratendinous" structure which could react to forces from several directions (i.e. as would occur with a distension of the mental region). Given the more vertical orientation of the grooves in the mental area, expansion would be confined primarily to that area and pooling of water would occur there. The fibrocartilage skeleton could reinforce the mental region against the stress of throat expansion in this region (Lambertsen & Hintz, 2004). We further envision the fibrocartilage skeleton as providing a flexible framework which could deform in a consistent, pre-determined way - the base of the skeleton swinging downwards and the branches outward. The ventral grooves which are crowded between the branches of the fibrocartilage skeleton in a swimming whale could open up freely as the branches diverged, allowing swelling of the mental region initially, then the rest of the ventral pouch.

More vertically oriented grooves occur in other rorquals. Even in the humpback whale, where there are fewer grooves, there are more vertically oriented grooves in the mental region (e.g. Chadwick & Nicklin, 1999: 110) so the mechanism we propose is feasible in all the rorquals. Thus we suggest that the rorqual throat region consists of two functional areas: (1) anterior inter-mandibular region with more vertically oriented grooves, fibro-cartilage skeleton and a localized capacity for expansion, and (2) rest of throat and ventral pouch, with longitudinally oriented grooves, leading primarily to an increase in circumference of the rest of the ventral pouch.

Lambertsen et al. (1995) and Lambertsen & Hintz (2004) suggested that a similar ballooning of the mental region could occur before the gulp through bringing the tongue forward; the expansion of the mental region would change

water flow around the head acting to preload the jaw structure for rapid opening and thus mimimization of a bow wave. This suggestion has been taken up as a feature of rorqual feeding in paleontological literature (Kimura, 2002). In those sequences in which we saw the lead up to the gulp, there was no evidence of such a deformation of the mental region. However the expansion of the mental region which we have observed at the beginning of the gulp sequence could serve at least some of the same functions as the preloading envisioned by Lambertsen et al. (1995). In particular, by providing a point of least resistance for inflow of water, it could minimize, and possibly eliminate, a bow wave effect at the beginning of the gulp.

At the beginning of the gulp, there was no evidence that the tongue was in the mental region; it would have been visible especially in gulp 1M4. However, at the end of the gulp cycle, we noted a forward traveling bulge along the throat region, which ended as a swelling in the mental area (1M3, Fig. 5B) similar to that seen at the beginning of inter-mandibular gulps. This is consistent with the mechanism suggested by Lambertsen (1983), i.e. a movement of the tongue anteriorly, expelling the last water from the oral cavity, thus minimizing the swallowing of seawater. An additional function seems possible. The forward movement of water could create a wash effect against the bristles of the baleen plates, helping dislodge any trapped prey. Partial depression of the floor of the oral cavity (as shown by the forwardly traveling bulge in the inter-mandibular area) might also create a reduction in pressure within the oral cavity, further aiding dislodgement of prey from the baleen bristles (cf. Werth, 2001). Deformation of the mental area would be through the same mechanism as indicated above – deformation of the fibrocartilage skeleton allowing an expansion of the overlying ventral pouch wall.

Whereas we note that the distension or ballooning of the mental region is primarily passive (driven by kinetic energy of forward locomotion of the body or of the tongue), during normal swimming the fibrocartilage skeleton could act as an anterior insertion point for the contracted longitudinal muscles of the ventral pouch, maintaining a taut and streamlined form in the throat region. Orton & Brodie (1987) suggested that these longitudinal muscles have a postural role, based on their finding that Type I (slow, oxidative) type fibres were extremely dominant in the ventral pouch region.

Finally, we note that our observations do not support the role of the fibrocartilage skeleton as a clamp, trapping anterior baleen plates against the mandibles and thus preventing loss of water around the baleen plates (Pivorunas, 1977); the fibrocartilage skeleton was always well removed from the anterior baleen plates while water was being expelled from the ventral pouch.

VERTICAL ANGLE OF JAWS DURING EXPULSION OF WATER. One striking feature of the gulp cycle is the small vertical separation of upper and lower jaws and thus the small area through which expulsion of water may take place, even including the groove or orolabial sulcus formed by partial alpha rotation of the lower jaw. One implication of this is that the area for egress of water is much smaller than the area of the fully expanded ventral pouch over which contraction takes place. By hydraulic theory, a small force over a wide area can be translated to a larger force over a small area. By this line of reasoning, the elastic energy per unit area of the ventral pouch may not have to be particularly high to force water through the baleen plates. As pointed out by Orton & Brodie (1987) it is unknown to what extent the muscles in a fully expanded ventral pouch could contract – at this stage the elastic fibres may provide the primary, if not exclusive, driving force. As the pouch contracts, the hydraulic power differential decreases and at this point muscles may become the main driving force in water expulsion.

EVOLUTION OF FILTER FEEDING: *opening of vestibulum oris*. A characteristic mammalian feature is the cheek which encloses a space, the vestibulum oris, bounded internally by the oral arch [if you lick the outside of your teeth, your tongue is protruding into this space]. As recognized by anatomists (e.g. Schulte, 1916; Pivorunas, 1976) the cheek structure has been lost in whales, creating an open vestibulum oris. One result is the reptilian appearance of the head of baleen whales, with the gape extending well posterior to the eye. This is accentuated in mysticete whales, especially rorquals, by fibrocartilage articulations at the mandibular symphysis and, especially, with the skull. This allows rotation of the mandibles and a virtual dislocation of the mandibles, to give an almost snake-like appearance with the diverging and laterally displaced mandibles of a gulping whale (Figs 6A,7A).

The opening of the vestibulum oris was an essential feature in the development of the

continuous suspension feeding of balaenids. In the right whales, a secondary cheek structure was developed with the greatly enlarged lip of the mandible, arching upwards and meeting the strongly arched, narrow rostrum. The fibrocartilage joint at the mandibular symphysis allows for some axial rotation of the mandible and lip. Rotation of the lower jaw swings the secondary cheek structure outwards, forming a groove just lateral to the long baleen plates, which is open at the back. Thus there is a discrete channel (orolabial sulcus: Werth, 2004a) through which water can continuously pass through the baleen plates and posteriorly. Werth (2004a) clearly demonstrated how hydraulic effects from flow in the orolabial sulcus could assist in passage of water through the baleen plates.

The role of the vestibulum oris is quite different in rorquals. In modern rorquals, the open vestibulum oris allows for the lateral displacement of the mandibles (omega rotation), especially if there is a capacity for its floor to expand. Morphological specializations which could allow this include the facial cleft noted by Pivorunas (1977) in common minke whales and the associated grooves overlying the mandible, both allowing a greater capture area by the axial rotation and lateral displacement of the mandibles. Delta rotation may be limited by the frontomandibular stay but lateral displacement would be limited by the extent to which the floor of the vestibulum oris can expand laterally near the angle of the mouth.

During contraction of the ventral pouch, water can escape laterally in any direction through the basal portion of the baleen plates exposed by the narrow gape (2-5°); a photograph by Nicklin (in Darling, 1995) of a common minke whale showed water squirting out from all along the baleen series. However, partial alpha rotation of the mandible (IM4, Fig. 3; IM3, Fig. 5) would also form a channel open posteriorly, through which water could be directed rearwards after passing between the baleen plates. This would be assisted by the backwards orientation of the slits between the baleen plates (Pivorunas, 1976), possibly assisted by a drop in pressure as water is expelled through the posterior open slit formed by the partially rotated mandible (Figs 3, 5). Thus hydraulic assistance of water egress could occur in rorquals, through mechanisms similar to those operating in balaenids (Werth, 2004a; Lambertsen et al., 2005 ), with the difference that it occurs episodically at the end of a gulp in rorquals rather than continuously as in balaenids. Such channeling of water is only possible due to the open vestibulum oris and loss of the classic mammalian cheek structure.

Sei whales are anomalous among the rorquals in that they have been described as both engulfment feeders and continuous skim feeders. Published direct observations of feeding are limited (Ingebrigtsen, 1929; Kawamura, 1974; Liouville in Andrews, 1914; Watkins & Schevill, 1979) and not always easy to interpret. Watkins & Schevill (1979) described sei whales as having their mouth wide open and closing slowly over a 20 second to 1 minute interval, which seems dysfunctional for engulfment feeding. Given the rapidity with which the oral cavity fills (even in non lunge-feeding events, see Table 1), keeping the mouth open for longer than a few seconds would result in a bow-wave effect. However, compared with other rorquals, the sei whale has a more strongly arched rostrum, down-turned at the tip (Leatherwood et al., 1988) and narrower, finely fringed baleen plates. It is possible that partial alphal rotation of the mandible and abduction of the lower jaw would form a channel more like that of the right whales, which would allow sufficient water to be ejected rearwards for continuous filtration. In this regard, Liouville noted that the sei whales he observed moved very slowly through the water, possibly allowing greater filtration of water through the finely fringed baleen plates. Ingebrigtsen, in contrast, noted that the sei whales moved quickly, with the baleen plates out of water. It is difficult to see how this could efficiently filter fine food, rather than creating a bow wave effect. Another possibility is that what Ingebrigtsen observed was not associated with feeding. We have seen dwarf minke whales with much of the rostrum and baleen plates free of the water (Fig. 9) when there was no concentration of food in the water and no evidence of feeding.

*Suction feeding as the primitive state?* Within mysticete lineages, the opening up of the vestibulum oris allowed for different developments, i.e. gulping of rorquals or the skimming of right whales. Gray whales represent a third development, suction feeding. Suction feeding involves expansion of the mouth volume, which can be accomplished by retraction of the tongue in a piston action and expansion of the throat, as by gular folds (Heyning & Mead, 1996). Suction feeding thus requires relatively little modification of the throat region.

Gular folds are found in at least some pygmy right whales and dwarf sperm whales, while they

are consistently present in the gray whale, the great sperm whale and most ziphiids. Suction feeding, at least for manipulation, if not capture, of food has been shown in gray whales (Ray & Schevill, 1974) and ziphiids (Heyning & Mead, 1996). A specialized form of suction feeding has been inferred for the sperm whale based on anatomy of the tongue and throat musculature: prey are sucked into the circular oropharyngeal opening, posterior to the oral cavity which is widely open through loss of cheeks and a closed vestibulum oris (Werth, 2004b). A form of suction feeding, at least in manipulating food, has also been demonstrated in delphinidan cetaceans – monodontids (beluga & narwhal), phocoenids (true porpoises) and delphinids (Werth, 2000). The widespread occurrence of gular folds and some form of suction feeding in such a range of extant odontocetes and baleen whales, representing diverse phylogenetic lineages (Messenger & McGuire, 1998; Nikaido et al., 2001), suggests that suction feeding occurred in earlier taxa of toothed whales, including those ancestral to baleen whales. Thus it would be the primitive condition for baleen whales.

The ventral grooves of rorquals are quite distinct from gular folds. As the foetus develop, one set of grooves appears under and posterior to the flipper, a second set develops at the throat and subsequently they coalesce (Ohsumi, 1960; Slijper, 1962). These grooves are distinct and more numerous than gular folds. For fossil mysticetes, it is impossible to determine if ventral grooves and associated elasticity of the throat and belly were present. However, two biomechanical analyses of feeding in the most derived fossil mysticetes (Bisconti & Varola, 2000; Kimura, 2002) suggested that jaw elevation and adduction were primarily through muscle action. An implication of that conclusion is that an elastic throat and ventral pouch, needed for gulp feeding, evolved more recently.

Reconstructions of early whales (e.g. Thewissen & Williams, 2002, fig. 2) show relatively little modification, however a form of suction feeding could exist as early as *Pakicetus* and certainly by the time of archaeocetes. Primitive baleen whales had a fibrous mandibular symphysis allowing axial rotation of the lower jaw, as required in all feeding types found in extant mysticetes. However, lateral mobility would be restricted by the high coronoid process which was still medial to the relatively well developed zygomatic arch (Fordyce & deMuizon, 2001, fig. 11).This, with the apparent lack of baleen, suggests that suction feeding would be the most likely feeding mode, perhaps comparable to that developed in present day beaked whales (Heyning & Mead, 1996). The next stage could be as envisioned for actiocetids by Deméré (2005), with baleen plates interspersed between widely spaced teeth. Either of the two other extant filtering modes (continuous filtration (skimming) of balaenids and neobalaenids; gulp feeding of balaenopterids) could have been derived from this suction feeding stage. However, in addition to axial rotation of the mandibles, gulp feeding requires additional specializations such as development of the elastic, highly distensible ventral pouch, specialized cranio-mandibular articulation, frontomandibular stay, possible re-orientation of mandibular condyles from dorsal to posterior position, lateral deflection of the coronoid process and capacity for extensive lateral displacement of the mandibles. Thus it represents the most derived form of suspension feeding seen in baleen whales.

FURTHER STUDIES. Our underwater observations have revealed two quite distinct types of gulps, inter-mandibular and full ventral pouch, which may have different functions. This flexibility in the form of gulps indicates a voluntary control of ventral pouch expansion which contrasts with previous models based on passive filling of the pouch. Further anatomical studies are needed on the myology of the entire ventral pouch to properly document the morphological specializations of gulp and lunge feeding. However more extensive studies on behaviour are also needed to document the extent to which the unique rorqual body plan has been exploited, not only for the high speed capture of prey but also for display and the social organisation of baleen whales.

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# PONTONIINE SHRIMPS FROM PAPUA NEW GUINEA, WITH DESIGNATION OF TWO NEW GENERA, *CAINONIA* AND *COLEMONIA* (CRUSTACEA: DECAPODA: PALAEMONIDAE)

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Bruce, A.J. 2005 12 31: Pontoniine shrimps from Papua New Guinea, with designation of two new genera, *Cainonia* and *Colemonia* (Crustacea: Decapoda: Palaemonidae). *Memoirs of the Queensland Museum* **51**(2): 333-383. Brisbane. ISSN 0079-8355.

A report is presented on a small collection of pontoniine shrimps, principally from the southern coast of Papua New Guinea, made by Neville Coleman in 2002-2003. The report includes information on 21 taxa, four of which are species new to science. These include one new species of a new genus, *Colemonia*, and three new species, *Periclimenes grandidens, Pontonides aspernatus* and *Pontonides loloata*. A new genus, *Cainonia*, is also designated for *Dactylonia medipacifica* (Edmondson), and two further new species are named, *Dactylonia borradailei* and *Pontonides sibogae*. Keys are provided to the genera of *Pontonia* sensu lato (Fransen, 2002) and species of *Pontonides* Borradaile. The pontoniine shrimp fauna of Papua New Guinea is reviewed. □ *Decapoda, Pontoniinae,* Cainonia *gen. nov.*, Colemonia *gen. nov., Papua New Guinea.*

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The early history of pontoniine shrimp studies in Papua New Guinean (PNG) waters is brief and is fully described by De Grave (2000), who provided details of 13 species at the beginning of the twentieth century, increasing to 71 by 2000. The present small collection was made mainly in the vicinity of Loloata Island, 9° 32.093'S, 147° 16.605'E, in the Port Moresby region of PNG, by Neville Coleman, as part of his studies for the Australian Marine Photographic Index. The report consists of 21 pontoniine shrimp taxa, 4 of which are undescribed species, but 3 can not be referred with certainty to any known species. Other specimens were collected from Milne Bay. Remarks are also included on some related taxa.

The pontoniine fauna of PNG's northern coastlines are relatively well known through studies based on the Hansa Bay region (De Grave, 1998a, 1988b, 1999, 2000), but the southern shores have been much less studied and the fauna is much less well known. The present study increases the number of species known from the southern coasts by 13. Restricted synonymies only are provided. Fuller synonymies are to be found in Li (2000).

ABBREVIATIONS, AMPI, Australian Marine Photographic Index; BM, Bishop Museum, Honolulu; CL, postorbital carapace length; KBIN, Koninlijk Belgisch Instituut voor Naturwetenschappen, Brussels; QM, Queensland Museum, Brisbane; RCL, rostral carapace length; RMNH, Nationaal Natuurhistorisch Museum, Leiden; USNM, National Museum of Natural History, Washington; ZMA, Zoological Museum, Amsterdam.

## SYSTEMATIC ZOOLOGY

Sub-phylum CRUSTACEA
Order DECAPODA Latreille, 1802
Family PALAEMONIDAE Rafinesque, 1815
Sub-family PONTONIINAE Kingsley, 1878

### **Colemonia** gen. nov.

DIAGNOSIS. Body form small, robust, subcylindrical. Rostrum short, acute, unarmed, with 2 preterminal setae dorsally, dorsal carina distinct, lateral carinae narrow; carapace glabrous, inferior orbital angle present, antennal spine acute, orbit feebly developed, supraorbital, epigastric and hepatic spines absent, anterolateral angle rounded, not produced. Abdomen with posterior segments depressed, pleura rounded, sixth segment with posterolateral angle acute, posteroventral angle enlarged, acute. Telson with two pairs of small marginal dorsal spines, three pairs of posterior spines. Eye normal, with hemispherical cornea. Antennule with strong ventromedial tooth on basal segment, anterolateral tooth well developed, not exceeding half length of intermediate segment, flagella reduced. Antenna with basicerite unarmed, scaphocerite small, with distolateral tooth not

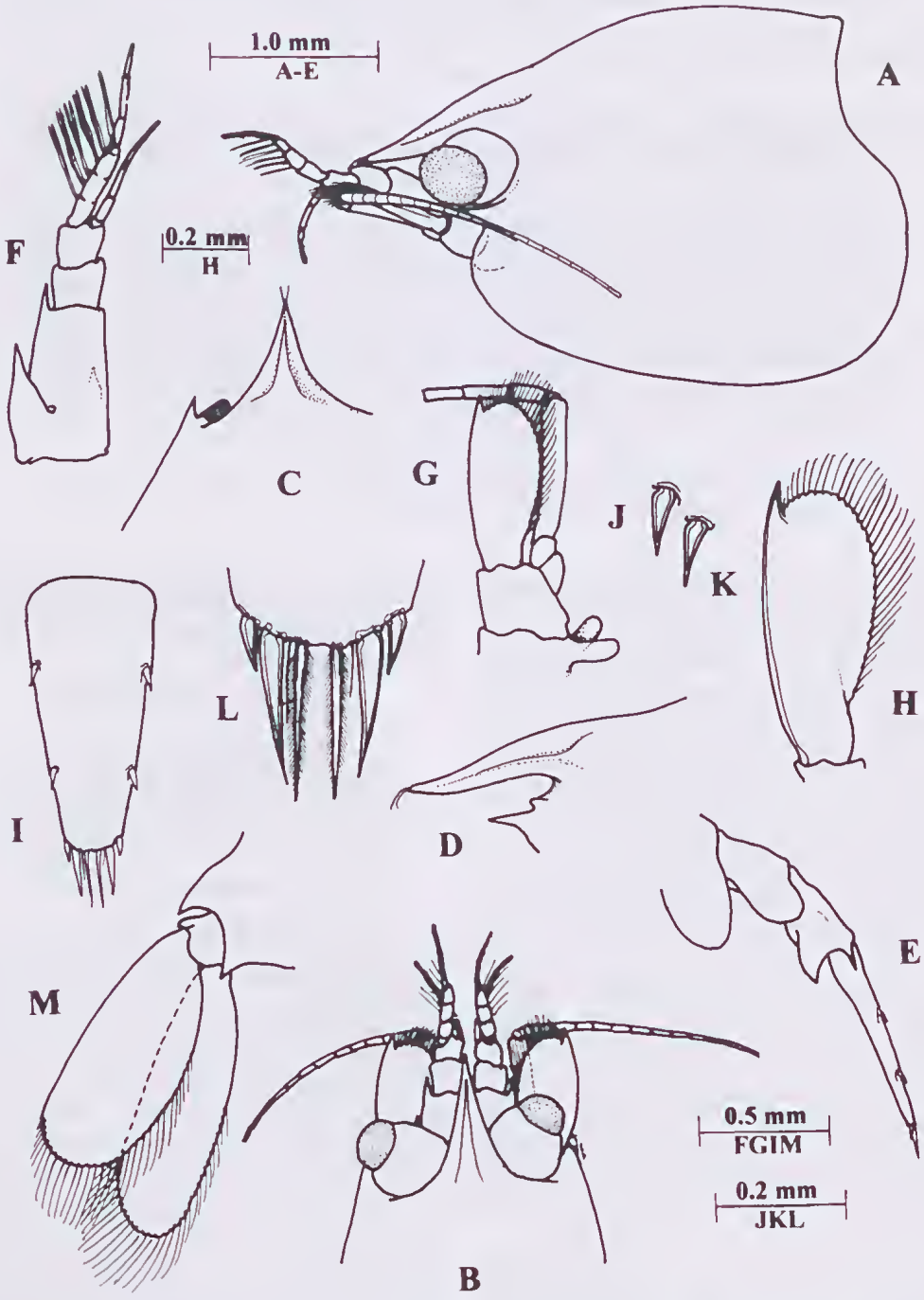


FIG. 1. *Colemonia litodactylus* gen. et sp. nov., holotype ♀, Madang. A, carapace and antennae, lateral. B, anterior carapace and antennae, dorsal. C, rostrum and left orbital region, dorsal. D, same, lateral. E, posterior abdominal segments and telson, lateral. F, antennule. G, antenna. H, seaphocerite. I, telson. J, same, anterior dorsal spine. K, same, posterior dorsal spine. L, posterior telson spines. M, uropod.

enlarged, less than 0.2 of lamellar length. Third thoracic sternite with large triangular transverse median plate, fourth unarmed, fifth with pair of low acute processes separated by median notch, sixth with low longitudinal median carina, seventh and eighth unarmed.

Mandible with slender corpus, without palp, molar process subcylindrical, incisor process with transverse set of four acute teeth distally, with denticles along medial border. Maxillula with bilobed palp, upper lacinia normal. Maxilla with enlarged, narrow simple basal endite with numerous setae medially, well exceeding slender palp, scaphognathite narrow. First maxilliped with slender setose palp, basal endite large, narrow, laterally convex, medially sublinear, with specialized distomedial setae (see description below), medial margin with sparse simple setae, distinct from rounded sparsely setose coxal endite, exopod well developed with narrow caridean lobe, flagellum with four plumose terminal setae, epipod large, bilobed. Second maxilliped endopod with dactylar segment small, basis with medial angulation, exopod flagellum well developed with four plumose terminal setae, epipod small, rounded with subacute posterior angle, without podobranch. Third maxilliped with ischiomerus fully fused to basis, endopod sub-operculiform, dorsally scaphoid, ante-penultimate segment much broader than distal segments, exopod flagellum well developed with four plumose terminal setae, coxa without medial process, with low rounded lateral plate, without arthrobranch. First pereiopods slender, with simple chelae. Second pereiopods with robust chelae, similar, slightly unequal, palm glabrous, smooth, without ventral carina, fingers without molar process and fossa, dactylus with single tooth, fixed finger with small acute tooth distally and denticulate carina proximally, both sparsely setose, proximal segments unarmed. Ambulatory pereiopods robust, dactylus simple, with unguis distinct, without distal scales, corpus without distoventral tooth or proximal accessory denticles, devoid of setae (except pair of disto- lateral sensory setae), propod with pair of well developed distoventral spines. Uropod with protopodite unarmed, exopod with distolateral spinule.

TYPE SPECIES. *Colemonia litodactylus* sp. nov.

ETYMOLOGY. For the collector, Neville Coleman, in recognition of his contribution to knowledge of the tropical shallow water marine fauna, and *Pontonia*, a name first used by Latreille (1829). Gender, feminine.

HOSTS. Associated with Ascidacea.

SYSTEMATIC POSITION. *Colemonia* is most closely related to *Dactylonia* and *Odontonia* Fransen (2002) (Table 1). The major differences between *Colemonia* gen. nov. and *Dactylonia* Fransen may be summarized as follows: In *Colemonia* the ventromedial tooth on the proximal segment of the antennular peduncle is large, the basal endite of the maxilla is elongate, narrow, simple, with numerous long setae, the basal endite of first maxilliped is elongate, narrow, sparsely setose, with some specialized apical spines, not forming a setal basket, the third maxilliped endopod has the articulation of ischiomerus and basis completely fused, broad, sparsely setose and semi-operculate, with a large transverse triangular sternal plate on the third thoracic sternite, the second pereiopod chelae subequal and similar, the third pereiopod with a simple dactylus, with only distolateral setae, and the telson with small dorsal spines.

The major differences between *Colemonia* gen. nov. and *Odontonia* Fransen may be similarly summarized as follows: In *Colemonia* the rostrum is acute, narrow with a distinct postrostral carina, the antennal spine is acute, the basal endite of the maxilla is elongate, narrow, simple, with numerous long setae, the basal endite of first maxilliped is elongate, narrow, sparsely setose, with some specialized apical spines, the third maxilliped endopod has the articulation of ischiomerus and basis completely fused, broad, sparsely setose and semi-operculate, with a large transverse triangular sternal plate on the third thoracic sternite, the second pereiopod chelae subequal, and the third pereiopod with a simple dactylus, with only distolateral setae, and strong distoventral propodal spines.

**Colemonia litodactylus** sp. nov.
(Figs 1-4, 22A )

MATERIAL. 1 ovig. ♀, AMPI 1450, # 28, Milne Bay, 12 m, April 2003, QMW27252.

DIAGNOSIS. Rostrum acute, low post-rostral carina, semi-operculate third maxilliped, with triangular median process between coxae, ambulatory dactyls with corpus completely unarmed ventrally, devoid of setae, third pereiopod propod with strong distoventral spines.

DESCRIPTION. Body robust, subcylindrical, smooth, glabrous. Rostrum (Fig. 1D) slender in

TABLE 1. Comparison of related genera of Pontoniinae. w/wo = with or without

| Character | *Dactylonia* | *Colemonia* | *Odontonia* |
|---|---|---|---|
| Rostrum | acute | acute | blunt |
| Rostral dentition | w/wo distoventral tooth | Nil | w/wo distoventral tooth |
| Lateral carinae | Narrow | Narrow | Broad |
| Postrostral region | Carinate | Carinate | Non-Carinate |
| Inferior orbital angle | Feebly developed | Distinct | Broadly rounded |
| Antennal spine | Acute | Acute | Blunt |
| Pterygostomial region | Rounded, not produced | Rounded, not produced | Rounded, not produced |
| Proximal antennular segment Ventromedial tooth | Small | Large | Large |
| Distolateral tooth | Reaching beyond middle of intermediate segment | Small | Large, reaching distal margin of intermediate segment |
| Anterolateral tooth of scaphocerite | <0.1 of scaphocerite length | about 0.12 scaphocerite length | >0.2 scaphocerite length |
| Incisor process of mandible, medial edge | Denticulate | Non-denticulate | Denticulate or non-denticulate |
| Basal endite of maxilla | Small, bilobed, proximal lobe sometimes obsolescent, sparsely setose | Large, elongate, narrow, simple, with numerous long setae | Small, bilobed or simple, sparsely setose |
| Basal endite of first maxilliped | Broad, very densely setose, forming basket | Elongate, narrow, sparsely setose, with few specialised apical spines | Broad, setose, not forming basket |
| Epipod of first maxilliped | Oval | Bilobed | Large, oval |
| Second maxilliped, dactylar segment | Long serrulate spines and setulose setae | Small, spines with filamentous setules | Short serrulate spines and long setulose setae |
| Basis | Without angular projection | Without angular projection | w/wo angular projection |
| Epipod | Rounded | Rounded, with posterior angulation w | Small, rounded or triangular |
| Third maxilliped, ischiomerus/ basis articulation | Partly fused | Fully fused | Partly fused |
| Combined segment form | Broad or narrow, not semi-operculate | Broad, semi-operculate | Narrow, not semi-operculate |
| Setation | Dense | Sparse | Moderate |
| Distal segments | Elongate, little narrower than combined segment | Short, broad, narrower than combined segment | Not short and broad |
| Terminal segment | Densely setose | Sparse short spines | Numerous serrulate setae |
| Third thoracic sternite | Unarmed | Large transverse triangular median plate | Unarmed |
| Fourth thoracic sternite | w/wo triangular notched plate | Unarmed | Transverse plate |
| Second pereiopod chelae | Unequal, dissimilar | Subequal, similar | Unequal, similar |
| Cross-section | Ventrally carinate, usually serrate | Oval, non-carinate, non-serrate | Oval, non-carinate, non-serrate |
| Dactylar dentition | Single tooth | Single tooth | Single tooth |
| Fingers | Gaping proximally | Not gaping | Not gaping |
| Dentition | Bidentate | Unidentate | Bidentate |
| Third pereiopod dactyl | Biunguiculate | Simple, unarmed | Usually biungniculate |
| Setation of corpus | Well-developed | Absent | Well-developed |
| Unguial microspinulation | Present | Absent | Present or absent |
| Propod, distoventral spines | Well-developed | Robust | Small |
| Ventral spines | Present | Absent | Absent |
| Sixth abdominal segment, posterolateral tooth | Acute, usually well-developed | Acute, slender | Blunt, reduced |
| Posteroventral tooth | Acute, small | Acute, broad | Blunt, reduced |
| Telson, dorsal spines | Very large, submarginal, generally grouped on anterior half of telson | Small, marginal, not grouped on anterior half of telson | Well-developed, not very large |

lateral view, tapering, acute, slightly exceeding intermediate segment of antennular peduncle, slightly depressed, unarmed, tip (Fig. 4A) with two long simple preterminal setae dorsally, ventral margin convex; in dorsal view (Fig. 1B,C), narrow, lateral carinae well developed, covering bases of eye stalks; with low narrow convex median dorsal carina, extending posteriorly to about level of posterior margin of orbit; carapace (Fig. 1A) with orbit weakly developed, inferior orbital angle small, rounded, antennal spine well developed, acute, marginal, extending well beyond anterior margin of carapace, pterygostomial region broadly rounded, not produced. Abdomen without special features. Pleura of first five segments broadly rounded; sixth segment (Fig. 1E) 0.31 of CL, depressed, posterolateral angle slender, acute, posteroventral angle broadly acute.

Telson (Fig. 1I) 0.6 of CL, about 2.2 times longer than sixth segment, about 2.2 times longer than anterior width, lateral margins sublinear, with 2 similar pairs of medium sized marginal dorsal spines (Fig. 1J,K), about 0.08 of telson length, at 0.33 and 0.66 of telson length, posterior margin (Fig. 1L) 0.4 of anterior margin width, broadly convex, with 3 pairs of spines, lateral spines small, about 0.35 of intermediate spine length, intermediate spines robust, about 0.17 of telson length, submedian spines slender, setulose, subequal to intermediate spine length.

Eyestalk (Fig. 1B, 4B) about 1.2 times longer than broad, 1.5 times broader than cornea; cornea hemispherical, poorly pigmented, diameter about 0.2 of CL, without distinct accessory pigment spot.

Antennule (Fig. 1F) normal; proximal segment of peduncle with large acute ventromedial tooth (Fig. 4B), distolateral tooth (Fig. 1F) well developed, about half length of intermediate segment, statocerite acute, reaching about 0.6 of segment length, statocyst normal, with subcircular statolith, sparsely setose laterally; intermediate and distal segments of subequal length; upper flagellum biramous with 3 stouter proximal segments fused, short ramus with single segment only, longer, with four slender segments, with about six groups of aesthetases, lower flagellum short, slender, with 4 segments.

Antenna (Fig. 1G) with basicerite robust, unarmed, antennal gland tubercle conspicuous, (single on right, doubled on left side); carpocerite about 6.8 times longer than wide, subcylindrical, slightly exceeding distal margin of lamella of scaphocerite; scaphocerite (Fig. 1H)) not reaching to end of antennal peduncle, narrow, about 2.5 times longer than wide, anterior margin rather rounded, lateral margin moderately convex, with relatively small distal tooth, about 0.12 of lamellar length, at about 9.12 of lamella length, extending distinctly beyond distal border of lamella.

Mandible (Fig. 2A) with corpus slender, without palp, incisor process (Fig. 4D) obliquely truncate distally, with 4 acute teeth, lateral tooth broadened, without denticles along distomedial margin; molar process (Fig. 4C) robust, centrally excavate with 4 blunt teeth, fringed by bands of short setae.

Maxillula (Fig. 2B) with stout feebly bilobed palp (Fig. 4E), proximal lobe small, with small hooked terminal seta; upper lacinia normal, with 7 short stout simple spines and setae distally, lower lacinia lost in dissection.

Maxilla (Fig. 2C) with slender subcylindrical non-setose palp, basal endite simple, large, broad, far exceeding palp, medially convex, distal and medial margin with numerous long, slender, sparsely setulose setae, coxal endite obsolete, medially concave; scaphognathite narrow, 3.5 times longer than central width, anterior lobe distally narrow.

First maxilliped (Fig. 2D) with short subcylindrical palp with preterminal simple seta, basal endite (Fig. 4F) well developed, narrow, about 1.7 times longer than basal width, well exceeding palp, lateral margin strongly convex, medial border straight, distomedial angle with single long simple fusiform terminal spine (Fig. 4G), with slightly shorter, more robust distally stellate spine (Fig. 4G) medially, with four shorter simple spines proximally, proximal medial margin with sparse long simple setae, coxal endite distinct, convex medially, non-setose, exopod well developed, flagellum with 4 plumose terminal setae, caridean lobe normal, epipod well developed, triangular, feebly bilobed.

Second maxilliped (Fig. 2E) with dactylar segment small, narrow, 3.2 times longer than wide, subequal to length of medial margin of propodal segment, with numerous long stout finely setulose setae (Fig. 4H), propodal segment large, twice as long as broad, distomedially rounded, with numerous stout denticulate spines medially, carpus, merus and ischiobasis without special features, exopod well developed with 4

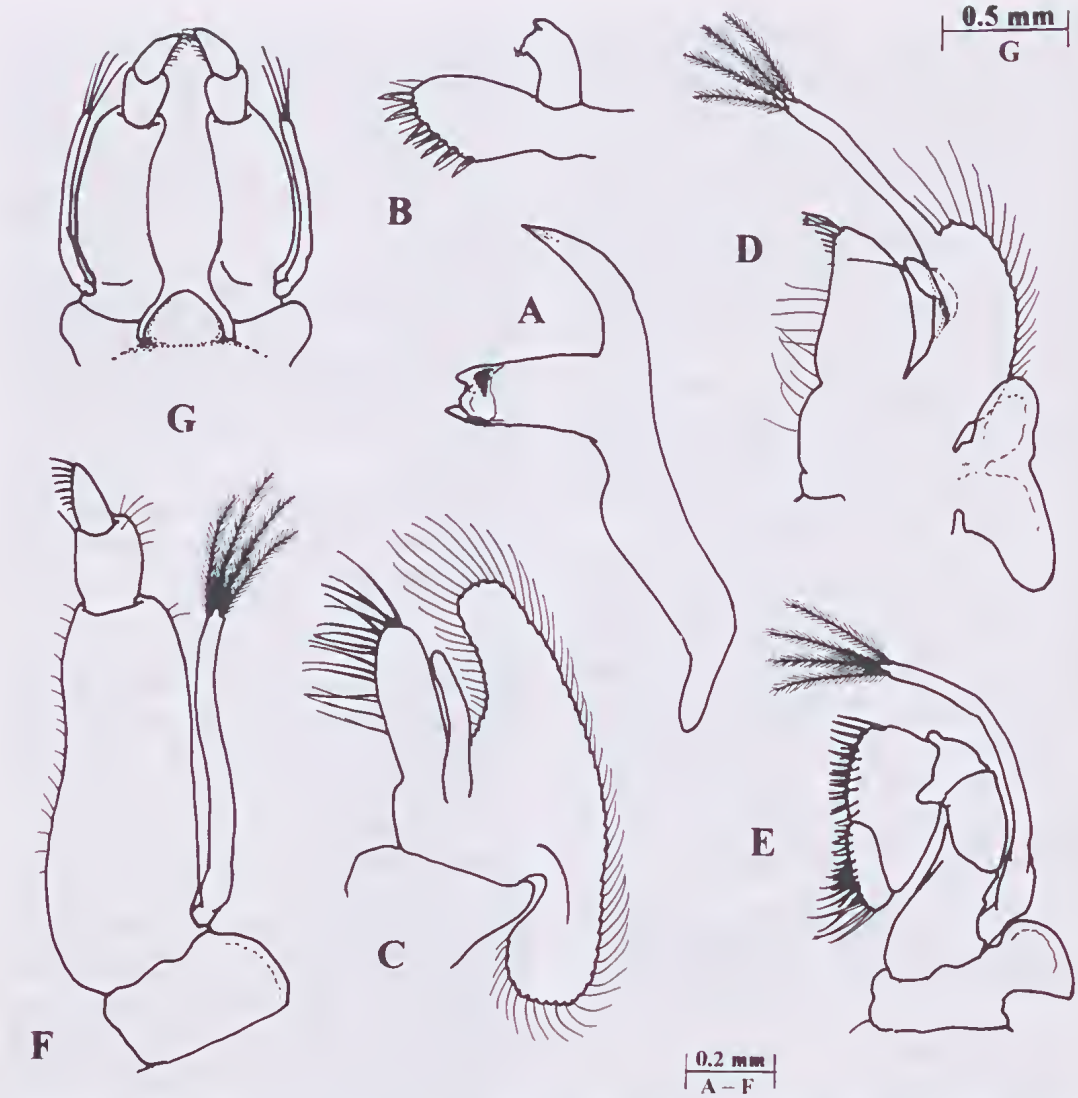


FIG. 2. *Colemonia litodactylus* gen. et sp. nov., holotype ♀, Madang. A, mandible. B, maxillula, upper lacinia and palp. C, maxilla. D, first maxilliped. E, second maxilliped. F, third maxilliped. G, third maxillipeds and third thoracic sternite.

plumose terminal setae, coxa with small rounded epipod, angularly produced posteriorly, without podobranch.

Third maxilliped (Fig. 2F) reaching to about distal basicerite, ischiomerus fully fused to basis without indication of demarkation, combined segment broad, semi-operculate, moderately scaphoid, 2.5 times longer than proximal width, feebly tapering distally, strongly bowed, medial margin with sparse short simple setae, lateral margin glabrous, penultimate segment short and broad, inserted slightly preterminally and sub-ventrally, about 0.25 of antepenultimate segment length, 1.4 times longer than wide, sparsely setose, terminal segment (Fig. 4I) preterminal, sub-ventrally inserted, 0.9 of penultimate segment length, 2.5 times longer than proximal width, tapering distally, with 2 short finely serrulate spines (Fig. 4I) medially, with largest spines distally, exopod well developed, reaching to end of isehiomeral segment, with 4 plumose terminal setae, coxa

normal with low rounded lateral plate, without arthrobranch. Paragnath (Fig. 4J) well developed; alae small, anteriorly rounded, posteriorly angular; corpus short, without carinae (?).

Third thoracic sternite with large transverse triangular plate, fourth unarmed, fifth with pair of low acute processes separated by median notch, sixth with low longitudinal median carina, seventh and eighth unarmed.

First pereiopod (Fig. 3A), exceeding basicerite by about half merus length; chela (Fig. 3B) about 3.0 times longer than deep, palm compressed, 1.5 times longer than depth, dorsally and ventrally convex, without cleaning setae proximally, with fingers subequal to palm length, compressed, dactylus slender, about 4.0 times longer than proximal depth, tapering strongly distally, to small simple acute hooked articulated unguis, cutting edge entire, sparsely setose, fixed finger similar; carpus slender, about 1.4 times chela length, 4.1 times longer than distal width, tapering strongly proximally; merus 1.2 times carpal length, 1.75 times chela length, 7.6 times longer than width, subuniform, slightly bowed; ischium about 0.5 of merus length; basis and coxa without special features.

Second pereiopods (Fig. 3C,F) well developed, slightly unequal in size, similar in shape. Major chela (Fig. 3D) about 0.97 of CL, palm slightly compressed, about 2.4 times longer than depth, tapering slightly distally, maximal depth at about 0.3 of length, smooth, glabrous, ventral margin not carinate, without serrations, fingers (Fig. 3E) about 0.33 of palm length, dactylus about 2.6 times longer than proximal depth, tapering distally to very strong acute hooked tip, with single small acute tooth at about half length, proximal and distal cutting edges entire; fixed finger about 1.25 times longer than proximal depth, ventrally non-carinate, cutting edge with small subacute tooth (Fig. 3E) at half length, distal cutting edge entire, with deep notch adjacent to tip, with low finely denticulate carina (Fig. 4K) proximally; carpus about 0.3 of palm length, 1.5 times longer than distal width, distally expanded, unarmed; merus 0.4 of palm length, uniform, 2.5 times longer than central width, unarmed; ischium subequal to carpus length, 3.0 times longer than distal width, tapering proximally.

Minor chela (Fig. 3G) about 0.89 of CL, 0.86 of major chela length, palm strongly compressed, about 2.5 times longer than depth, glabrous, ventral margin non-carinate, without serrations, fingers (Fig. 4H) about 0.3 of palm length, dactylus about 3.5 times longer than proximal depth, with single small acute tooth proximally at about 0.5 of length, distal cutting edge entire, tip strongly hooked, acute; fixed finger 1.5 times as long as proximal depth, cutting edge similar to that of major chela but less developed; carpus about 0.38 of palm length, 2.6 times longer than distal width, unarmed; proximal segments similar to major chela, less robust

Third pereiopod (Fig. 3I) exceeding carpocerite by about 0.3 of propod length. Dactylus (Fig. 4L) about 0.22 of propod length, corpus compressed, about 1.8 times longer than proximal depth, dorsal margin convex, ventral margin feebly concave, without distal accessory or other teeth, with pair of well developed sensory setae distolaterally, otherwise completely glabrous, unguis about 0.45 of corpus length, 1.8 times longer than basal width, transversely articulated with corpus, subacute, curved, without micro-denticulations. Propodus (Fig. 3J) about 0.5 of CL, subcylindrical, sparsely setose, about 6.6 times longer than proximal width, with pair of well developed distoventral spines, length almost subequal to basal width of dactylar corpus, ventral margin without spines; carpus about 0.5 of propod length, 3.0 times longer than distal width, tapering slightly proximally, unarmed; merus subequal to propod length, 4.4 times longer than central width, unarmed; ischium about 0.8 of propod length, unarmed; basis and coxa without special features. Fourth and fifth perciopods similar.

Uropod (Fig. 1M) with short unarmed protopodite, exopod 2.3 times longer than broad, lateral margin convex, without distolateral tooth (Fig. 4M), with small mobile distolateral spine, without distinct diaeresis, endopod about 1.1 times exopod length, 3.3 times longer than wide.

Ova numerous and small, about 100.

MEASUREMENTS (mms). Postorbital carapace length, 2.2; carapace and rostrum, 3.2; body length (approx.), 9.5; major chela, 3.30; minor chela, 2.85; length of ovum, 0.75 .

COLOURATION (From colour transparency, AMPI 1450). Body and appendages semi-transparent, finely speckled with minute white chromatophores; with white median dorsal stripe along whole body, extending onto eyestalks, expanded over hepatic region of carapace and on each abdominal segment, with similar narrow band of white on second pereiopods along ventral margin of dactylus, palm of chela, carpus, merus and ischium.

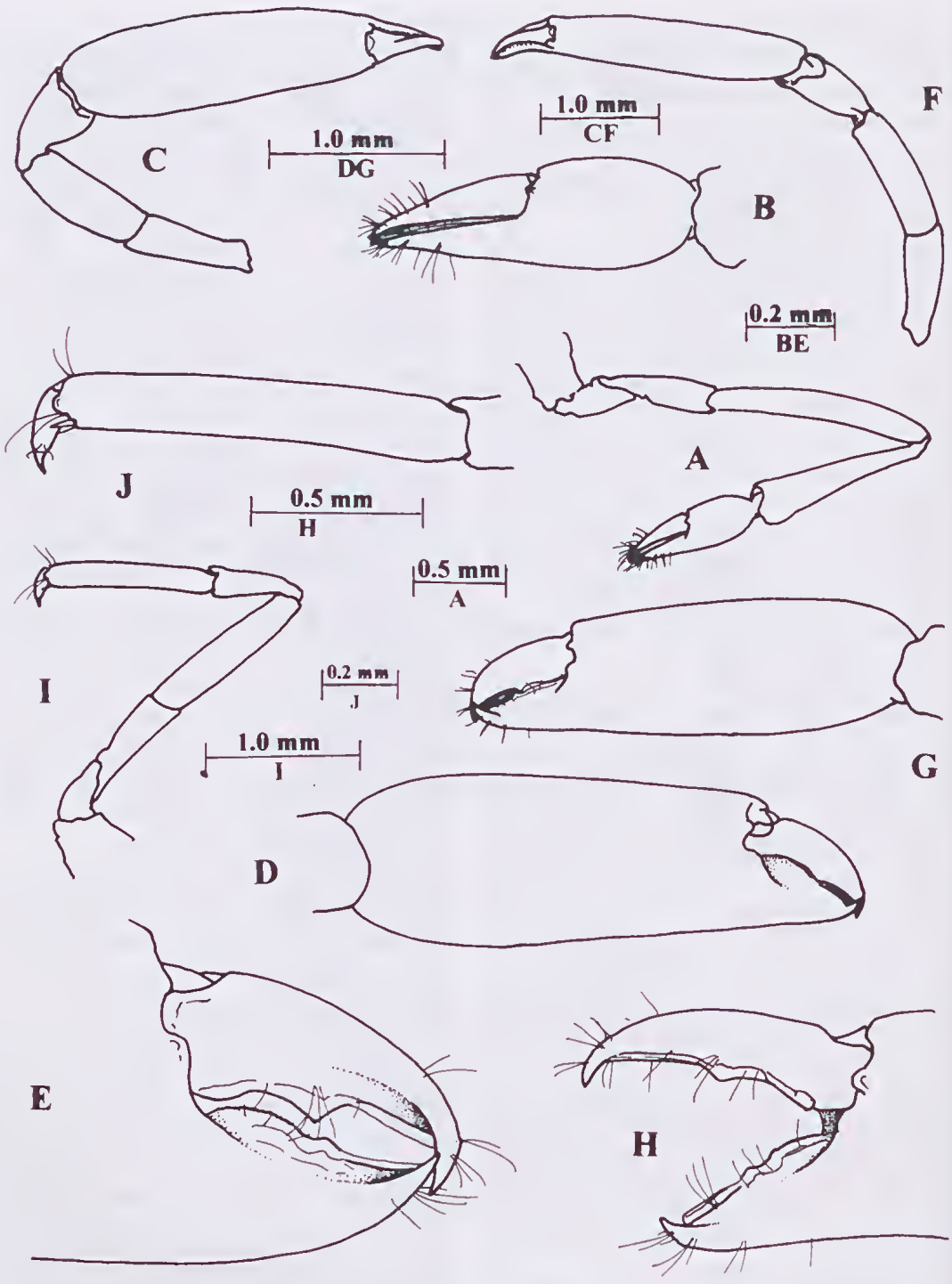


Fig. 3. *Colemonia litodactylus* gen. et sp. nov., holotype ♀, Madang. A, first pereiopod. B, same, chela. C, major second pereiopod. D, same, chela. E, same, fingers. F, minor second pereiopod. G, same, chela. H, same, fingers. I, third pereiopod. J, same, propod and dactylus.

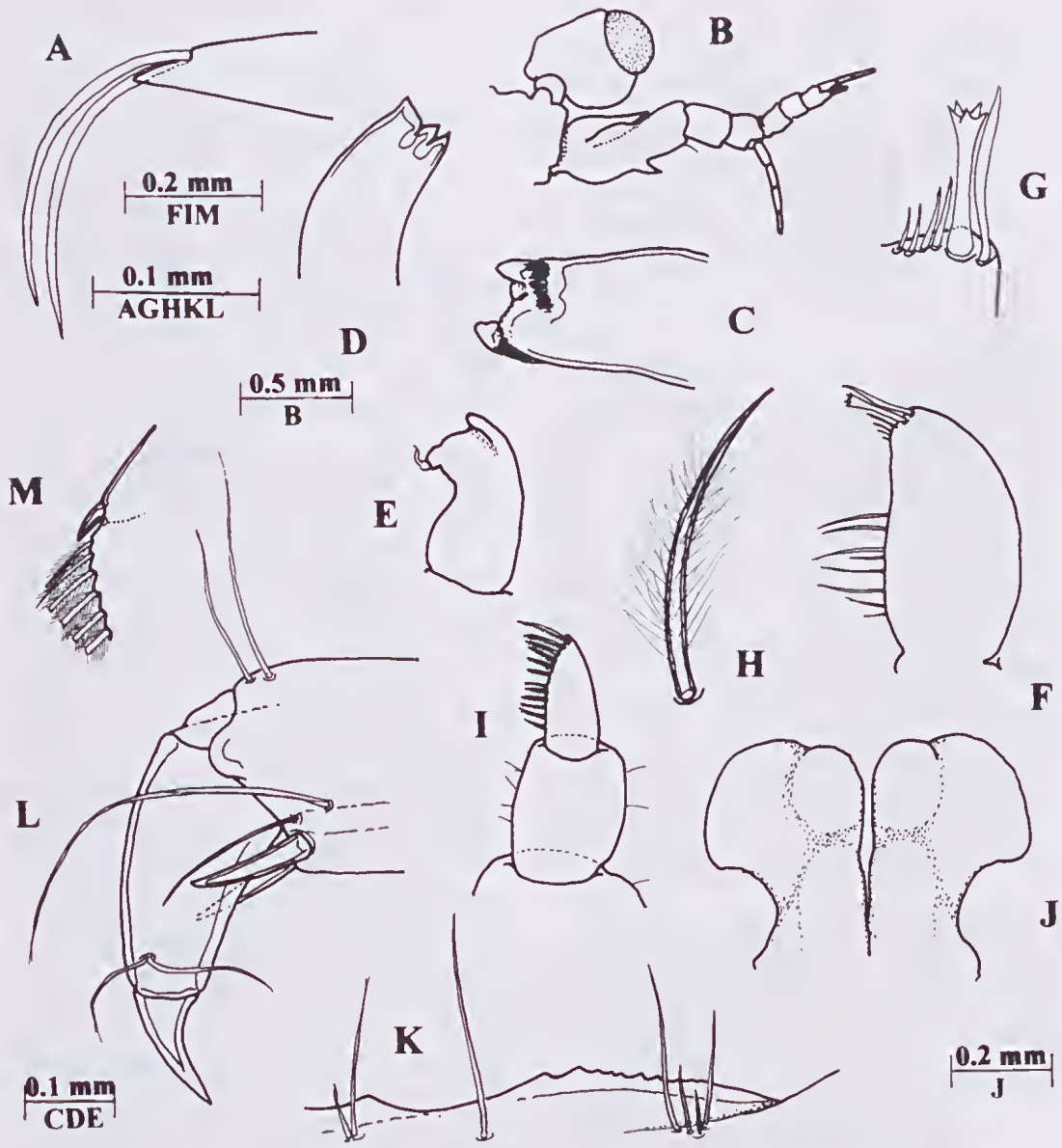


FIG. 4. *Colemonia litodactylus* gen. et sp. nov., holotype ♀, Madang. A, tip of rostrum. B, left eye, ophthalmic somite and antennule, medial aspect. C, mandible, molar proeess. D, same, incisor proeess. E, maxillula, palp. F, first maxilliped, endopod. G, same, terminal spines. H, seeond maxilliped, dactylar seta. I, third maxilliped, endopod, terminal and penultimate segments. J, paragnaths. K, minor seeond perciopod, proximal cutting edge of fixed finger. L, third pereiopod, distal propod and daetylus. M, uropod, exopod, posterolateral spine.

HOST. Unidentified encrusting ascidian, [Ascidiacea].

ETYMOLOGY. Greek, *litos*, simple, and *daktylos*, finger

REMARKS. The accompanying male was lost during photography. Although no carinae were observed on the corpus of the paragnath prior to dissection, it is possible that these were overlooked as the paragnath was damaged during removal.

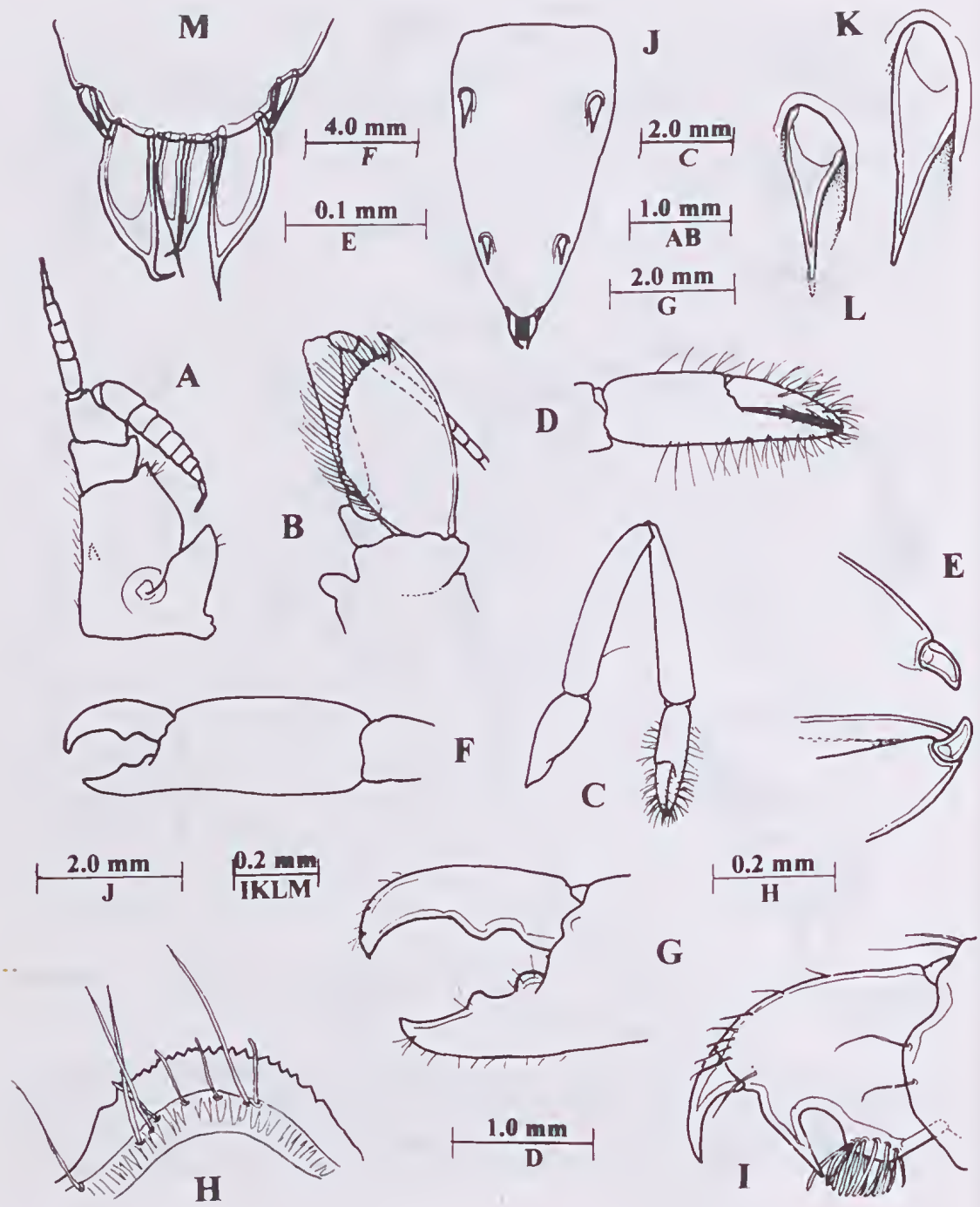


FIG. 5.*Conchodytes meleagrinae* Peters, ovig ♀, Milne Bay. A, antennule. B, antenna. C, first pereiopod. D, same, chela. E, same, finger tips. F, second pereiopod, chela. G, same, fingers. H, same, fixed finger, proximal tooth. I, third pereiopod, dactylus. J, telson. K, same, anterior dorsal spine. L, same, posterior dorsal spine. M, same posterior spines.

### Conchodytes meleagrinae Peters, 1852a (Fig. 5)

*Conchodytes meleagrinae* Peters, 1852a: 594; 1952b: 288; Li, 2000: 25, fig. 268; Davie, 2002: 308.
*Conchodytes tridacnae* Holthuis, 1952: 195, fig. 95 (*partim*); Jayachandran, 2001: 248, fig. 63 (*partim*).

MATERIAL. 1 ovigerous ♀, AMPI 1372, Milne Bay, 10 m, November 2002, QMW.27278.

REMARKS. The exact collection details, including the host, are uncertain. The specimen is referred to *C. meleagrinae* as the dorsal telson spines are at about 0.24 and 0.75 of the telson length, although the first pereiopod carpus is subequal to the merus length as is more approximate to the condition in *C. tridacnae* Peters.

Few illustrations of *C. meleagrinae* are available in the literature and the original descriptions (Peters, 1852a,b) were without illustration. Pearson (1905), Borradaile (1917), and Kemp (1922) also provided unillustrated reports. Nobili (1906) illustrated only the ambulatory dactyl. The first more comprehensive description and illustrations were provided by Kubo (1940), of specimens from the Ryukyu Islands, in *Tridacna* hosts, and from Palau, from *Pinctada* hosts. Kubo's figures for *C. meleagrinae* indicate that the first pereiopod carpus is distinctly shorter than the merus in that species and that the dorsal telson spines are at about 0.25 and 0.73 of the telson length. More recently Li (1997) has also figured the telsons of *C. meleagrinae* and *C. tridacnae* and shown again that the posterior dorsal spines of *C. tridacnae* are more posteriorly placed than those of *C. meleagrinae*. Britayev & Fachrutdinov (1994) indicate about 0.2 and 0.89 in *C. tridacnae* from Vietnamese waters.

The present specimen, CL 10.2 cm, referred to *C. meleagrinae*, agrees closely with the information provided by Kubo. The following points may be noted. The antenna (Fig. 5A) has a small ventromedial tooth on the proximal segment, the distolateral angle is produced and acute, the stylocerite is also distally acute, the upper flagellum is biramous with the first 5 segments fused, short ramus with 2 free segments, with about 6-7 groups of aesthetases, longer ramus with 3 free segments, lower flagellum with 7 segments. The antenna (Fig. 5B) has the carpocerite 6 times longer than wide, well exceeding scaphocerite lamella and its distolateral tooth; scaphocerite lamella 1.7 times longer than wide, distolateral tooth large, far exceeding long axis of lamella. First pereiopod (Fig. 5C) with carpus and merus subequal, chela (Fig. 5D) with fingers subequal to palm length, with numerous groups of long serrulate setae, small stout articulated tips (Fig. 5E), surrounded by short stout simple setae, cutting edges entire. Second pereiopods subequal, chela (Fig. 5F) subequal to CL, palm about twice as long as deep, tapering slightly distally, fingers (Fig. 5G) about half palm length, dactylus compressed, non-carinate dorsally, with single acute denticulate tooth, fixed finger similar, with two denticulate teeth (Fig. 5H). Third pereiopod dactylus (Fig. 5I) has a robust articulated curved unguis, about 0.5 of the dorsal length of the corpus, corpus strongly compressed, distodorsal region with submarginal setae, accessory tooth large, acute, subequal to unguis, basal process without tooth, with numerous short stout simple setae, propod without spines. Telson (Fig. 5J) about 1.8 times longer than anterior width, dorsal spines well developed, anterior spines (Fig. 5K) about 0.12 of telson length, at 0.24 of telson length, posterior spines (Fig. 5L) smaller, about 0.75 of anterior pair length, at 0.75 of telson length, posterior margin narrow, convex, without median process, about 0.25 of anterior width, posterior spines (Fig. 5M) marginal, lateral spines small, about 0.35 of posterior dorsal spine length, intermediate spines proximally inflated, distally attenuated, about 0.11 of telson length, subequal to posterior dorsal spine length, submedian spines more slender, about 0.6 of intermediate spine length, non-setulose.

DISTRIBUTION. PNG – Previously reported from Hansa Bay, 5-15m, in *Pinctada margaritifera* and *P. maxima* (De Grave, 1999). Other – Type locality: Ibo, Cabo Delgado, Mozambique. Also reported from Egypt, Yemen, Kenya, Moçambique, Madagascar, Seychelle Islands, Oman, Maldive Islands, Sri Lanka, Andaman Islands, Malaysia, Indonesia, Vietnam, China, Japan, Northern Territory, Queensland, Caroline Islands, Marshall Islands, New Caledonia, Fijian Islands, Cook Islands, Tuamotu Islands, and Hawaiian Islands.

### Dasycaris zanzibarica Bruce, 1973

*Dasycaris zanzibarica* Bruce, 1973: 247, figs 1-6; 1991b: 265, fig. 27; Li, 2000: 45, fig. 46; Davie, 2002: 310.

MATERIAL. 1♂, 1 ovigerous ♀, AMPI 1458, # 118, Loloata Island, 15 m, 22 April 2003, QMW27247.

HOST. *Cirripathes* sp. indet. [Antipatharia].

REMARKS. The specimens agree closely with earlier descriptions. The dorsal teeth on the carapace are very well developed, with the

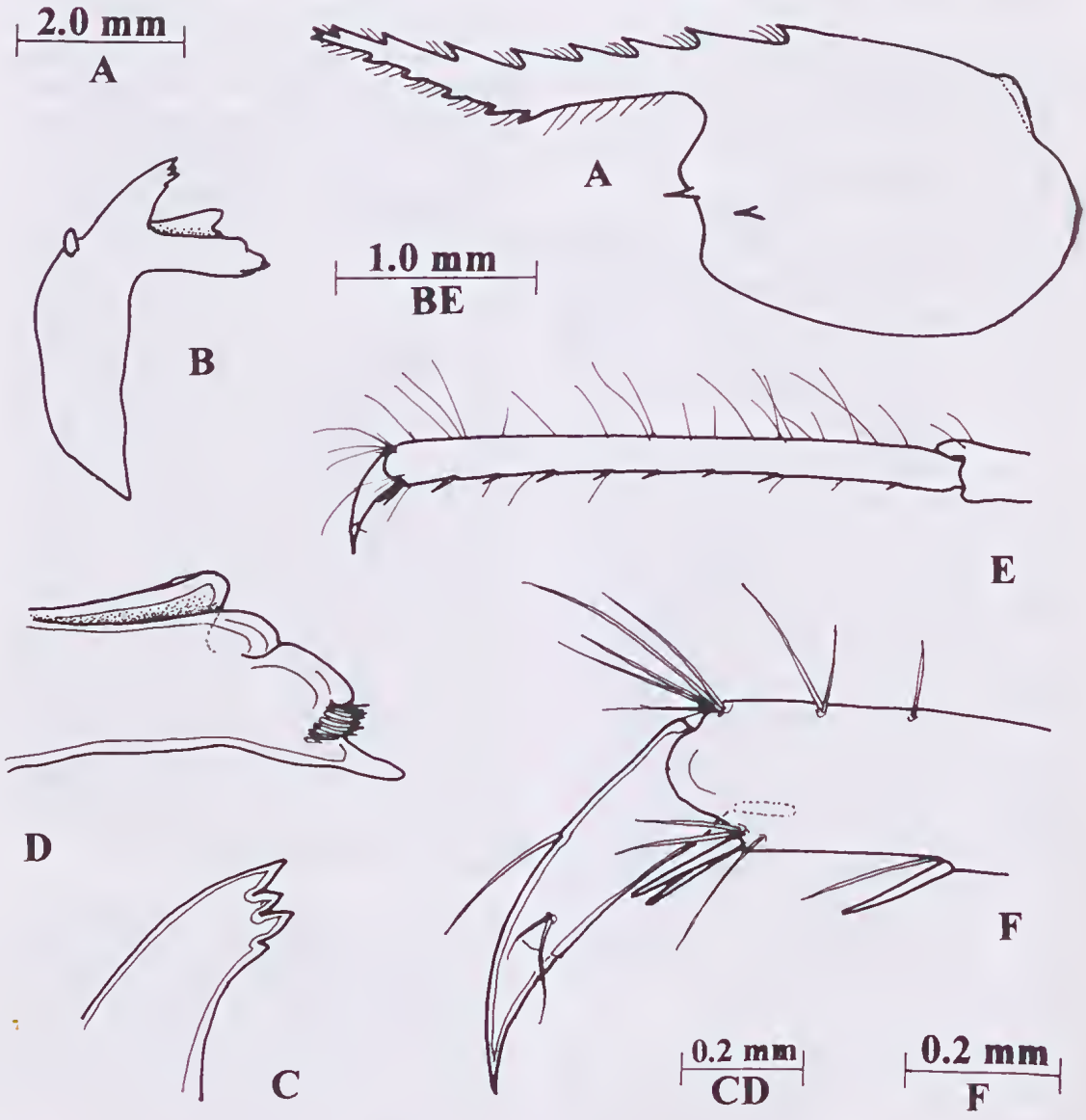


FIG. 6. *Exoclimenella* aff. *maldivensis* Duris & Bruce, ovig. ♀, Milne Bay. A, carapace and rostrum. B, mandible. C, same, incisor process. D, same, molar process. E, third pereiopod, propod and dactyl. F, same, distal propod and dactyl.

anterior tooth almost completely post-orbital. In the male the rostrum reaches almost to the end of the antennular peduncle, in the female, only to the end of the proximal peduncular segment.

DISTRIBUTION. PNG – Loloata Island (Coleman, 1998) and Madang, to 41 m (Debelius, 1999). Other – Type locality: Changu Island, Zanzibar. Also reported from Queensland, Taiwan, Japan, Philippines and New Caledonia.

**Exoclimenella** aff. **maldivensis** Duris & Bruce, 1995
(Figs 6, 22B)

MATERIAL. 1 ovigerous ♀, AMPl 1465, # 15, Milne Bay, 8 April 2003, QMW27254.

.COLOURATION (From colour transpareney, AMPl 1465). Body generally semitransparent; posterior margin of earapaee with broad dark band with white spots, hepatopanereas (?) with submedian and lateral white patehes; eyestalk, eornea, ophthalmie somite and bases of antennal pedunele bright red; seeond pereiopods densely spotted with small white dots, with dark band aeross eentral earpus, four similar bands on palm, fingers with dark longitudinal striae; eaudal fan with dark transverse band eentrally.

HABITAT. Under algae.

REMARKS. The single speeimen, has a single detaehed first pereiopod and laeks both second pereiopods. It has a rostral dentition of 1+8/5 (Fig. 6A), antennal and hepatie spines, but laeks a supraorbital spine, a finger-like median proeess is present on the fourth thoraeie sternite, the fifth sternite with a bidentate transverse ridge, and a small single segmented non-setose palp on the mandible (Fig. 6B). Two arthrobranehs are present on the third maxilliped, each with four bilobed lamellae. The first pereiopod ehela is strongly subspatulate, with dentieulate eutting edges to the fingers, daetylus with a transparent distolateral lamina. The posterior margin of the third abdominal tergite is entire, without miero-denticulations. The speeimen therefore readily fits into the diagnosis of *Exoclimenella* as provided by Duris & Bruce (1995), with the exeeption of the absenee of mierodentieulations from the third abdominal tergite. Without seeond pereiopods it cannot be eertainly identified with any of the described speeies of *Exoclimenella*. However, *E. sudanensis* Duris & Bruce, 1995. ean be exeluded from eonsideration on aeeount of it having a supraorbital spine and *E. sibogae* (Holthuis, 1952) on aeeount of the quite dissimilar rostrum. Both *E. maldivensis* Duris & Bruee, 1995, and *E. denticulata* (Nobili,1906) would be exeluded by their having well developed dentieulations on the posterior margin of the third abdominal tergite and it is eonsidered most likely that this speeimen represents an undeseribed taxon.

Other morphologieal features may be noted. The rostrum has two dorsal teeth distally anterior to the level of the most distal ventral tooth. A distinet post-orbital ridge is present, elose to the anterior margin of the orbit and the antennal spine is marginal. The eorpus of the mandible in this speeimen is robust and the molar proeess (Fig. 6D), is partieularly stout and broad, but the ineisor proeess (Fig. 6C), is eomparatively feeble and narrow rather than broad and has a small additional tooth on the distomedial margin. The fourth pleuron is posteroventrally rounded, the fifth aeutely pointed. The third pereiopod is similar to that of *E. maldivensis*: the ventral margin of the daetylus (Fig. 6F), is uniformly eoneave, and the anterior margin has a single long seta at 0.37 of the length. The unguis is more than half the eorpus length. The propod (Fig. 6E), has a pair of distoventral spines and 8 ventral spines. The speeimen agrees elosely with the speeimen reported from Haehijo Island, Japan, exeept that that speeimen shows a distinetly post-marginal antennal spine. This speeimen also laeks dentieulation on the posterior margin of the third abdominal tergite (Okuno, pers. eomm., 3 November 2003).

The eolour pattern of this speeimen eorresponds exaetly with that illustrated by Kawamoto & Okuno (2003:30) as *E. maldivensis* from Kume Island, Okinawa and also with *E. maldivensis* by Debelius (1999: 189, from the Burma Banks, Thailand), whieh also shows the reddish eyes and has dark purplish patehes on the ehelae of the seeond pereiopods as deseribed in *E. maldivensis* by Duris & Bruee (1995, fig. 5 ab).

Colouration of *E. denticulata, E. sudanensis, E. sibogae* and *E. maldivensis* s.str. are still unknown.

DISTRIBUTION. PNG – Laing Island and Wanginam Bay, Hansa Bay, 15 m, in *Seriatopora hystrix* (De Grave, 2000). Other – Type locality: Genego Islet, North Nilandu Atoll, Maldive Islands. Also reported from Thailand, Japan and Western Australia.

**Kemponia** sp. aff. **agag** (Kemp, 1922)
(Fig. 7)

*Periclimenes (Ancylocaris) agag* Kemp, 1922: 197, figs 47-49, pl. 7.
*Periclimenes agag*; Li, 2000: 150, fig. 181; Jayachandran, 2001: 281, fig.75; Davie, 2002,: 323.
Not *Periclimenes agag*; Bruce, 1992: 64, fig. 16.
*Kemponia agag*; Bruce, 2004: 10.

MATERIAL. 1 ♂, 1 ov.♀, AMPl 1452, #68, Loloata Island, 18 m, 12 April 2003, QM W27253.

DIAGNOSIS. A small speeies of the *grandis*-group *sensu* Kemp (1922) now placed in

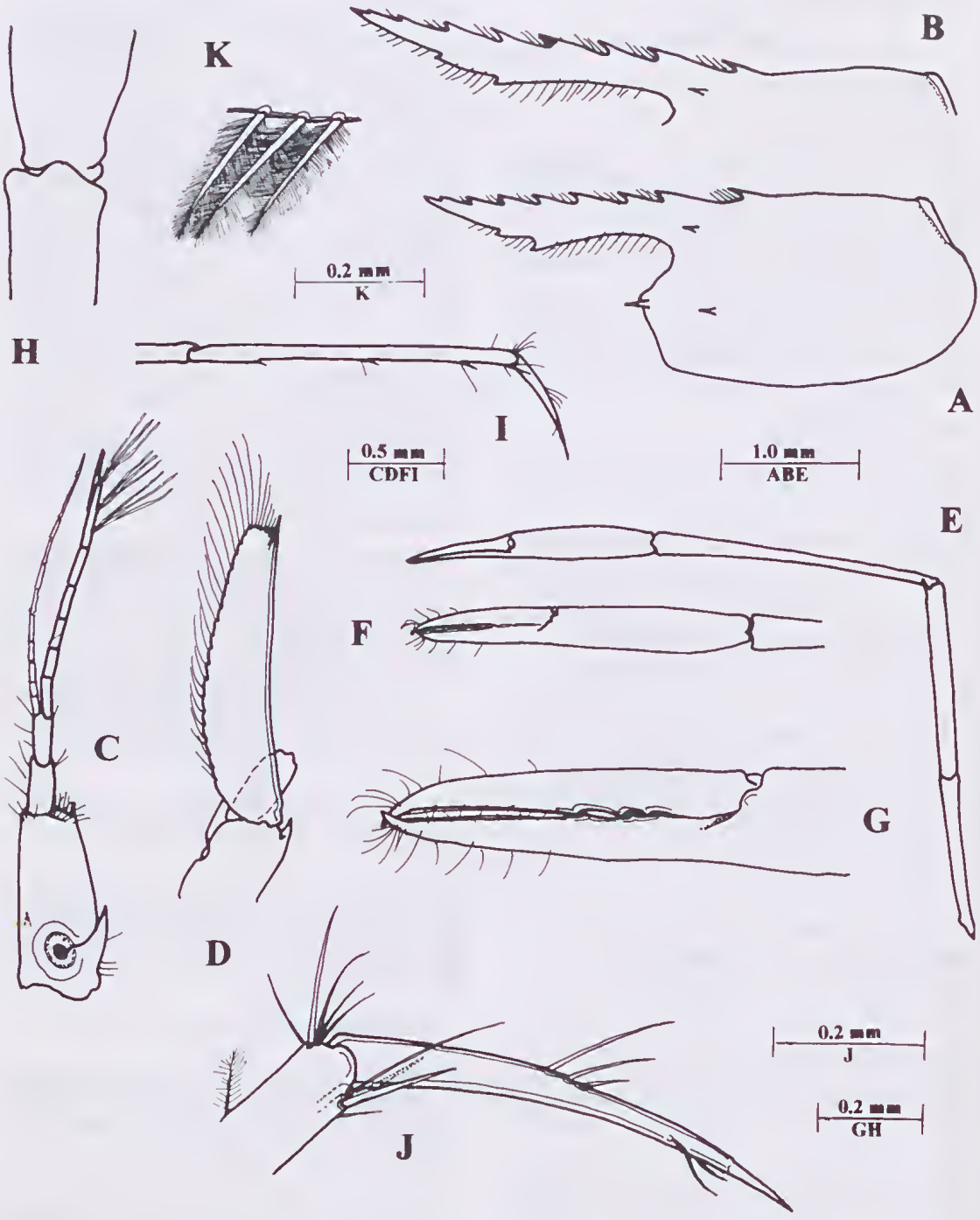


FIG. 7. *Kemponia* aff. *agag* (Kemp). A, carapace and rostrum. B, rostrum. C, antennule. D, antenna. E, second pereiopod. F, same, chela. G, same, fingers. H, same, distal carpus. I,. third pereiopod (?), propod and dactyl. J, same, distal propod and dactyl. K, ventral pleural setae. A,C,D,I, ovigerous ♀. B, ♂.

*Kemponia* Bruce. Rostrum shallow (♂) (Fig. 7B), deeper (♀) (Fig. 7A), reaching to end of scaphocerite, 0.95 (♀)-1.2 (♂) of CL, dentition 1+7/2, first tooth on carapace, with supraorbital, antennal and hepatic spines, inferior orbital angle reduced; posterior margin of third abdominal tergite minutely denticulate, pleura 4-5 posteriorly blunt; scaphocerite (Fig. 7D) with distolateral tooth well exceeding lamella; eye stout, cornea 0.25 of CL; mandible without palp, third maxilliped with small arthrobranch; fourth thoracic sternite with slender median process; first pereiopod with carpus 1.85 times chela length; second pereiopod (Fig. 7E) slender, chela subequal to CL, palm smooth, fingers (Fig. 7G) about 0.75 of palm length, feebly excavate, weakly dentate (Fig.7G), 3 small teeth proximally on dactylus, 2 on fixed finger, distal cutting edges entire, sharp; carpus greater than chela length, distally unarmed; third pereiopod propod (Fig. 7I) subequal to CL, with distoventral spines twice basal width of dactylus, with 3 shorter ventral spines, dactyl (Fig. 7J) slender, about 0.28 of propod length, 9.0 longer than basal width.

MEASUREMENTS. Carapace length, 1.8 (♂), 2.0 (♀) mm.

COLOURATION (From colour transparency, AMPI 1452). Body and antennae semitransparent, feebly speckled with small white dots, pinkish patches, on ventral abdomen (?), second pereiopods with palms of chelae pinkish, fingers white.

HOST. *Cavernularia glans* [Pennatulacea]. The association may have been accidental.

REMARKS. The small specimens are accompanied by only a single detached second pereiopod, there are also three detached ambulatory pereiopods. The female has no attached pereiopods and the male has both first pereiopods and the right fifth pereiopod, with the right second pereiopod regenerating.

Kemp (1922) remarked of the *P. grandis* group, (now *Kemponia*) that "The species of this group are more difficult to identify than any others of the subfamily". This situation has not greatly improved since Kemp's time. The present specimens are referred with some hesitation to Kemp's *P. agag*. The antennular upper flagellum is biramous (Fig. 7C) with the six proximal segments fused, the short ramus consists of only a single segment and the longer of two, only three groups of aesthetascs are present. The scaphocerite (Fig. 7D) is similar to that illustrated by Kemp. The only second pereiopod (Fig.7E) preserved may be that of the female, which is less useful than that of the male for the purposes of species identification. The second pereiopod carpus (Fig. 7H), in particular, has only a single small blunt distal lobe, not two as in Kemp's material. The minute denticulations along the posterior margin of the third abdominal tergite is similar to that reported in *Exoclimenella* and *Periclimenella* species by Duris & Bruce (1995, fig. 7D), but which have not yet been reported in any other species of *Kemponia* or *Periclimenes*. The ventral margins of the pleura are provided with numerous conspicuous very densely plumose setae (Fig. 7K), an unusual feature in the *grandis* species group. The collection of further specimens is necessary to confirm or refute the identification and the association with a pennatulacean. The present specimens are not conspecific with the specimens reported, as *P. agag*, from Lizard Island, Queensland (Bruce, 1992), which may belong to *K. longirostris* (Borradaile) (see Holthuis, 1958). They also differ from Ledoyer's New Caledonian material, which had the fifth pleuron posteroventrally acute and not rounded (Ledoyer, 1984, as *P. (Harpilius) agag*).

The species of the *P. grandis* group, *sensu* Kemp, now included in *Kemponia*, appear to be free-living micro-predators, without "commensal" associations. The exception is *Kemponia amymone* (De Man), a coral associate. The association of the present specimens with a pennatulacean may have been accidental, but the occurrence of a heterosexual pair suggests that it may have been genuine. Associations of *Periclimenes* species with shallow water pennatulaceans have not been reported but do occur in deeper water, i.e., *Periclimenes alcocki* Kemp, 1922, with *Virgularia* sp. at 620-666m (Bruce, 1996).

DISTRIBUTION. PNG – *Kemponia agag* s.str. has not been reported from PNG. Other – Type locality: Port Blair, Andaman Islands. Reported from Red Sea, Andaman Islands, Marshall Islands and (?) New Caledonia.

### **Manipontonia psamathe** (De Man, 1902)

*Urocaris psamathe* De Man, 1902: 816, pl. 25, fig. 51.
*Periclimenes (Ancylocaris) psamathe*; Kemp, 1922: 173.
*Periclimenes (Harpilius) psamathe*; Holthuis, 1952: 61, fig. 23.
*Periclimenes psamathe*; De Grave, 2000: 139; Li, 2000: 229, fig. 304; Davie, 2002: 331.
*Manipontonia psamathe*; Bruce et al., 2005: 6-8, figs 1-3.

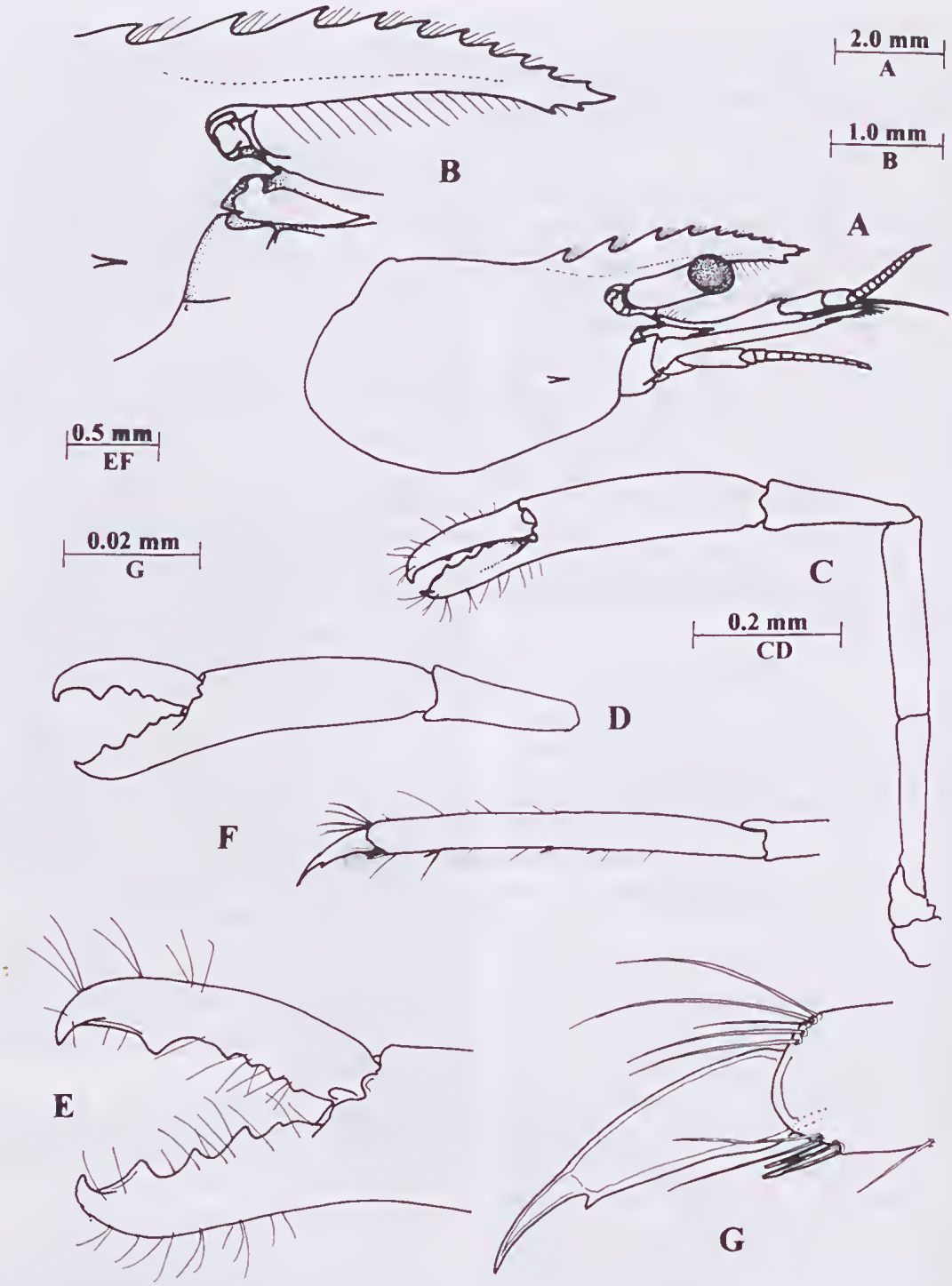


FIG. 8. *Periclimenes grandidens* sp. nov., ovig. ♀, holotype. A, carapace and rostrum. B, anterior carapace and rostrum. C, major second pereiopod. D, same, chela. E, same, fingers. F, third pereiopod, propod and dactyl. G, same, distal propod and dactyl.

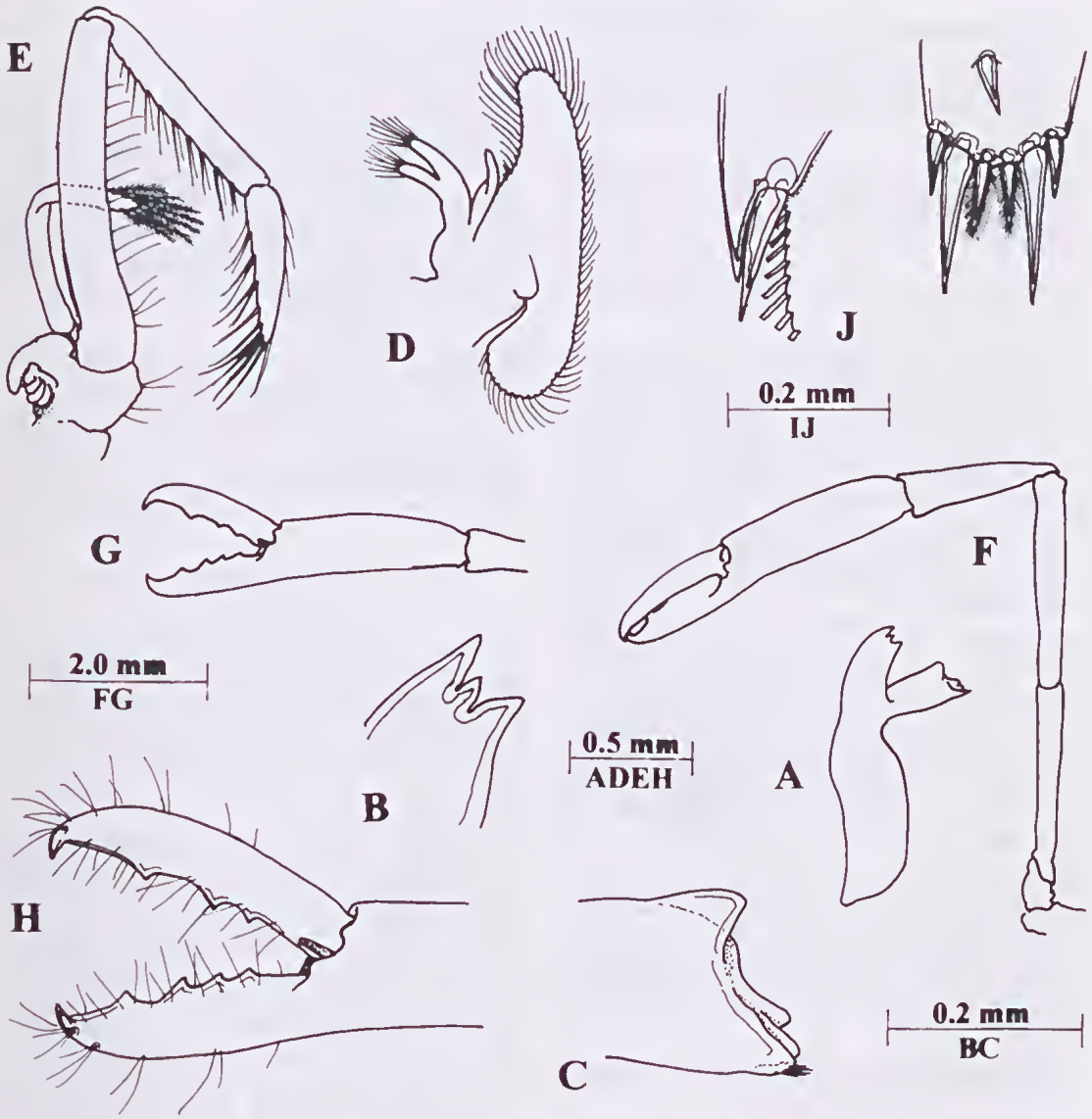


FIG. 9. *Periclimenes grandidens* sp. nov., ovig. ♀, paratype. A, mandible. B, same, molar process. C, same, incisor process. D, maxilla. E, third maxilliped. F, minor second pereiopod. G, same, chela. H, same, fingers. I, posterior telson spines. J, uropod, distolateral angle of exopod.

MATERIAL. (1) 1♂, AMPI ???, # 144, Loloata Island, 24 April 2003, QMW27244. (2) 1♀, AMPI 1454, # 119, Loloata Island, 22 April 2003, QMW27233.

HOST. (2) *Junceella* sp. [Gorgonacea].

REMARKS. (2) with both second pereiopods in early regeneration. The specimens present no special features. Rostral dentitions, 1+2+ ??/0.

DISTRIBUTION. PNG – Sushi Maru Wreck; Duangit reef, Hansa Bay, 19-42 m, (De Grave, 2000). Other – Type locality: Ternate, Indonesia. Also known from Kenya, Zanzibar, Tanganyika, Madagascar, Seyehelle Islands, Maldive Islands, Chagos Islands, Singapore, Malaya, Indonesia, South China Sea, Japan, Phillipines, Queensland, New Caledonia, Caroline Islands, Marshall Islands.

### Periclimenes amboinensis (De Man, 1888)

*Anchistia amboinensis* De Man, 1888: 546, pl. 22a, fig. 2.
*Periclimenes amboinensis*; Borradaile, 1898: 385; Bruce, 1992: 64, fig. 16; De Grave, 2000: 133; Li, 2000: 153, fig. 187; Davie, 2002: 323.

MATERIAL. (1) 1 ov.♀, AMPI 1459, # 101, Loloata Island, 10 m, 20 April 2003, QM W27251. (2) 1 ov.♀, AMPI 1453, # 84, Milne Bay, 10 m, 19 April 2003, QM W27250.

HOST. (1) *Comanthina* sp. (2) unidentified crinoid, [Crinoidea].

COLOURATION (From colour slide, AMPI 1459). Body and appendages very dark blue-black, body with numerous narrow transverse bars of dark gray, distal rostrum, eyes, tips of fingers of second pereiopods, patches along ambulatory pereiopods and tips of caudal fan all bright yellow. (From colour slide, AMPI 1453). Body and appendages deep red, with numerous paler pinkish patches and spots, cornea brilliant white.

REMARKS. (1) Rostral dentition 7/2. (2) The specimen lacks most of the rostrum, so the identification must be considered provisional only. A colour photo shows that about 6-7 dorsal teeth were present, ventral teeth cannot be discerned. From the photographs taken the hosts appear to be different crinoids, so the specimens may represent two closely similar species.

DISTRIBUTION. PNG – Madang (Debelius, 1999) and, Laing Islands; Duangit reef; and Wanginam reef; Hansa Bay, 10-30 m (De Grave, 2000). Other – Type locality: Ambon, Moluccan Islands, Indonesia. Known also from Maldive Islands, Thailand, Indonesia, Taiwan, Japan, Western Australia, Queensland, Marshall Islands, and New Caledonia.

### Periclimenes ceratophthalmus Borradaile, 1915

*Periclimenes (Corniger) ceratophthalmus* Borradaile, 1915: 211; 1917: 324, 365, pl. 54 fig. 9.
*Periclimenes (Ancylocaris) ceratophthalmus*; Kemp, 1922: 172.
*Periclimenes (Periclimenes) ceratophthalmus*; Kemp, 1925: 324, fig. 18.
*Periclimenes ceratophthalmus*; De Grave, 2000: 134; Li, 2000: 167, fig. 206; Davie, 2002: 325.

MATERIAL. 1♀, AMPI 1457, # 117, Loloata Island, 10 m, 22 April 2003, QMW27249.

HOST. Unidentified crinoid.

COLOURATION (From colour transparency, AMPI 1457). Dark red, almost uniform, with feeble slightly paler longitidinal banding, palest on exopod of uropod, which is mottled with transparent patches.

REMARKS. The specimen, CL 2.6 mm, presents no special features and has a rostral dentition of 3/0, and the small dorsal telson spines are subequal to the lateral posterior spines, about 0.1 mm in length, 0.05 of the telson length. The single second pereiopod has the chela about 1.15 times the CL. The colour pattern is similar to but darker than that shown by Debelius (1999) for a Tongan specimen.

DISTRIBUTION. PNG – Kimbe Bay (Debelius, 1999) and Mast Wreck; Wanginam reef and Awar Wreck, Hansa Bay; 4-15 m (De Grave, 2000). Other – Type locality: Hululé, North Malé Atoll, Maldive Islands. Known also from Red Sea, Kenya, Zanzibar, Seychelle Islands, Maldive Islands, Indonesia, Japan, Queensland, New South Wales, Solomon Islands, Tongan and Caroline Islands.

### Periclimenes grandidens sp. nov. (Figs 8-10, 22C)

MATERIAL. (1) 1 ovigerous ♀, holotype, AMPI 1445, # 91, Loloata Island, 16 m, 19 April 2003, QM W27245. (2) 1 ovig. ♀, paratype, AMPI 1446, # 141, Loloata Island, 23 April 2003, QM W27246. (3) 1 ♀, paratype, AMPI 1400, Loloata Island, 20 m, November 2002, QM W27238. (4) 2 juv.♀♀, AMPI 1460, # 133, Loloata Island, 23 April 2003, QM W27239.

DIAGNOSIS. A species of the *holthuisi*-group, rostrum normal, arched; dentition 1+8-9/2-3, without epigastric tooth, third abdominal tergum posterodorsally produced, bluntly subcarinate, ophthalmic somite without *bec ocellaire*, second pereiopod with carpus about 0.75 of palm length, chelae not bowed, fingers distinctly shorter than palm, with 3-4 large acute teeth distributed over whole length of cutting edges, third pereiopod propod with short spines, dactyl about 3.5 times longer than basal width, about 0.2 of propod length, with small projecting accessory tooth.

DESCRIPTION. A slenderly built shrimp of the *holthuisi*-species group, of subcylindrical body form, with a relatively well developed abdomen.

Rostrum (Fig. 8B) well developed, about 0.95 of CL, slightly elevated, weakly arched, compressed, reaching to near distal margin of intermediate antennular peduncle segment, lateral and ventral carinae absent, dorsal carina well developed with 9-10 acute teeth, first tooth situated posterior to orbital margin, size and separation diminishing distally, ventral margin concave, with long plumose setae, with 1-3 small acute teeth distally. Carapace (Fig. 8A) smooth,

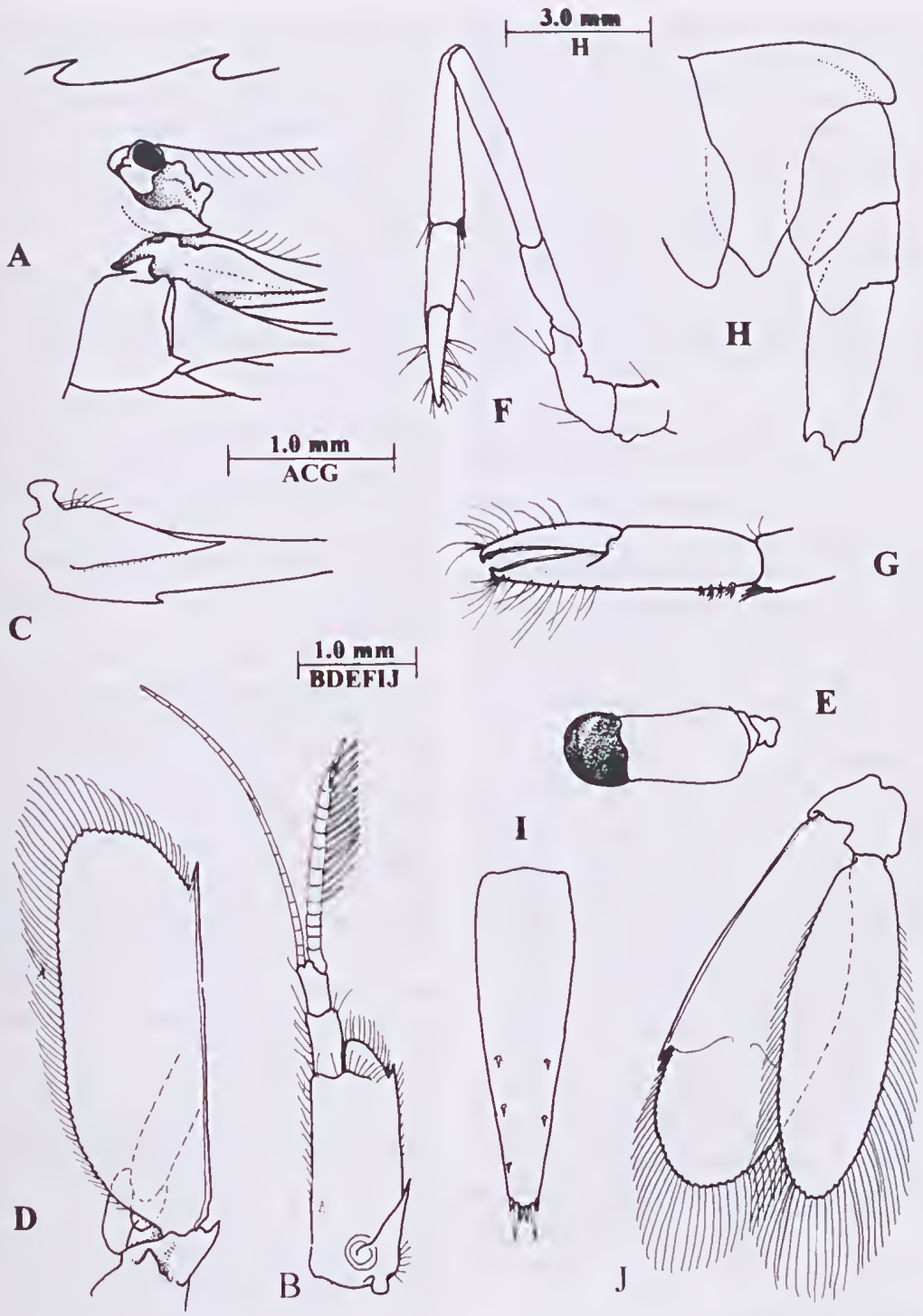


FIG. 10. *Periclimenes grandidens* sp. nov., ovig. ♀, paratype. A, anterior carapace, lateral. B, antennule. C, same, proximal segment of right pedunele, lateral. D, antenna. E, eye. F, first pereiopod. G, same, chela. H, third to sixth abdominal segments. I, telson. J, uropod.

glabrous, without epigastric tooth or supraorbital spines, orbit weakly developed, inferior orbital angle (Fig. 10A) strongly produced, acute, dorsally convex, with inner ventral flange, antennal spine small, marginal, hepatic spine larger, placed below level of antennal spine, anterolateral branchiostegite broadly rounded.

Abdomen well developed, smooth, glabrous, third tergite (Fig. 10H) bluntly produced posteriorly, sixth segment about twice length of fifth, twice as long as anterior depth, posterolateral and posteroventral angles acute, pleura of first to third segments bluntly elongated ventrally, fourth and fifth bluntly produced posteriorly.

Telson (Fig. 10I) about 0. 9 of CL, 0.85 of sixth abdominal segment length, about 3.5 times longer than anterior width, lateral margins sublinear, converging posteriorly, with two pairs of small dorsolateral spines at about 0.6 and 0.7 of telson length (asymmetrical in holotype), posterior margin (Fig. 9I) about 0.3 of anterior telson width, angular, without median point, with three pairs of spines, lateral spines robust, about 0.45 of telson length, intermediate spines longer, about 2.5 times length of lateral spines, submedian spines slightly longer than lateral spines, more slender and densely plumose.

Antennule (Fig. 10B) with proximal segment about 2.5 times longer than wide, medial and lateral margins subparallel, with numerous plumose setae, anterolateral margin strongly produced, obliquely rounded, reaching to middle of intermediate segment, densely setose, anterolateral tooth small, reaching to about one third of the anterolateral lobe length, proximal dorsolateral angle with conspicuous rounded protuberance (Fig. 10A,B,C), ventromedial margin with small acute tooth (Fig. 10C) at 0.3 of length; stylocerite well developed, acute, slender, reaching to about 0.45 of segment length, statocyst normal; intermediate segment about 0.3 of proximal segment length, twice as long as wide, densely setose medially; distal segment about 0.8 of intermediate segment length, 2.1 times longer than distal width; upper flagellum biramous, rami with proximal 10 segments fused, shorter ramus with 3 free segments, longer ramus with about 10, with about 18 groups of aesthetases, longer ramus filiform, about 1.5 times peduncle length.

Antenna (Fig. 10D) with stout basicerite with small acute ventral distolateral tooth, with angular process proximodorsally(Fig. 10A,D), carpocerite subcylindrical, reaching to about 0.5 of scaphocerite length, flagellum well developed; scaphocerite large, exceeding antennular peduncle, about 3.0 times longer than width, lateral margin straight, subparallel to medial margin, with small acute distolateral tooth far exceeded by obliquely rounded distal lamella.

Ophthalmic somite with small rounded *bec ocellaire*.

Eye (Fig. 10E) well developed, with large globular cornea, about 0.2 of CL, without ocellus, stalk subcylindrical, slightly tapering distally, about 1.8 times maximal width.

Epistome unarmed.

Mouthparts as in *P. holthuisi* Bruce. Mandible (Fig. 9A) small, without palp; molar process (Fig. 9B) distally obliquely truncate with 4 blunt teeth; incisor process (Fig. 9C) with three acute teeth distally, central tooth smallest, medial margin without denticles. Maxilla (Fig. 9D) with bilobed palp, each lobe with about 8 simple setae. Third maxilliped (Fig. 9E) coxa with rounded lateral plate, with small quadrilamellar arthrobranch.

Fourth thoracic sternite unarmed.

First pereiopod (Fig. 10F) slender, exceeding distal margin of scaphocerite by fingers; chela (Fig. 10G) subequal to carpal length, palm slightly compressed, about 2.5 times longer than deep, with 4 transverse rows of short coarsely serrulate spines proximoventrally, fingers with numerous setae, subequal to palm length, slender, tapering, with stout hooked tips, cutting edges entire, lateral; carpus about 4.6 times longer than distal width, tapering slightly proximally, with serrulate setae distoventrally; merus about 1.2 times carpal length, subcylindrical, 7.5 times longer than width; ischium about half meral length; basis and coxa without special features.

Second pereiopods (Fig. 8C) well developed, similar, slightly unequal. Major chela (Fig. 8D) about 1.02-1.19 of CL, not bowed, palm smooth, oval in section, about 3.2 times longer than deep, slightly enlarged distally, fingers (Fig. 8E) robust, about 0.6 of palm length, dactylus 4.6 times proximal depth, with stout hooked tip, cutting edge lateral, with large blunt tooth at about 0.75 of length, separated by broad notch from four smaller proximal teeth, distal cutting edge entire, fixed finger similar, with three large blunt teeth, more evenly distributed, and smaller more recurved tooth proximally; carpus about 0.6 of palm length, subequal to finger length,

about 4.0 times longer than central width, weakly expanded distally, unarmed; merus unarmed, about 0.85 of palm length, 5.2 times longer than central width; ischium almost subequal to meral length; basis and coxa without special features. Minor second pereiopod (Fig. 9F) similar to major chela, with chela (Fig. 9G) about 0.89-0.92 of CL, 0.76-0.91 of major chela length, palm 3.3 times longer than central depth, fingers (Fig. 9H) about 0.75 of palm length, dactylus with three well developed acute teeth, fixed finger with four, both extending over the central half of the cutting edges, posterior three teeth of fixed finger slightly recurved; carpus about 0.8 of palm length; merus 1.2 times palm length; ischium subequal to palm length.

Third pereiopod reaching to distal end of scaphocerite; dactylus (Fig. 8G) about 0.23 of propod length, with corpus compressed, 2.5 times longer than basal width, tapering distally to half basal width, dorsal margin weakly convex, ventral margin feebly concave, with small acute distal accessory tooth, about 0.12 of unguis length, unguis feebly demarkated from corpus, slender, curved, 4.0 times longer than basal width; propod (Fig. 8F) about subequal to CL, uniform, about 11.5 times longer than wide, with pair of short distoventral spines, subequal to basal width of dactylus, three similar isolated spines along ventral border; carpus about 0.5 of propod length, merus subequal to propod length, ischium 0.5 of propod length; fourth and fifth pereiopods similar.

Uropod (Fig. 10J) far exceeding telson, with protopodite posterolaterally unarmed; exopod broad, about 2.7 times longer than greatest width, at about half length, lateral margin non-setose, weakly convex, with long slender posterolateral tooth (Fig. 9J), with longer mobile spine medially, diaresis poorly demarkated; endopod about 0.9 of exopod length, 3.2 times longer than central width.

MEASUREMENTS (mm). Holotype ♀, carapace length, 4.7; carapace and rostrum, 7.8; total body length (approx.), 26.0; second pereiopod, major chela, 4.8; minor chela, 4.3; length of non-eyed ovum, 0.5. Paratype female, carapace length, 3.9; length of eyed ovum, 0.85.

HOSTS. (1)(2) *Euphyllia paradivisa* Veron, 1990; (3) *Plerogyra sinuosa* (Dana) [Scleractinia, Caryophyllidae]. (4) *Stichodactyla mertensii* Brandt [Actininaria].

COLOURATION (From colour transparency, AMPI1445). Body and appendages mainly semi-transparent, thoracic region with sparse larger white spots with small closely associated deep blue spots, abdomen with large conspicuous broadly U-shaped patch on posterior third tergite, with central white patches, surrounded by deep blue patches, outlined narrowly by white, second tergite with dorsolateral white spot surrounded by blue, margined narrowly with white, fourth tergite with contiguous submedian white spots, surrounded by blue and margined narrowly with white, posterior sixth segment whitish; telson proximally deep reddish, distally white, terminally deep blue; antennal peduncles and scaphocerite colourless, antennal flagella white; eyestalk with two dorsal white spots, cornea golden; first and second pereiopods with joints deep blue, carpus, merus and palm spotted with small white dots, fingers white; ambulatory pereiopods colourless; uropods with distal two thirds deep blue outlined by white marginal band, broadest anteriorly, endopod with white dots proximally; ova pale pink.

SYSTEMATIC POSITION. *Periclimenes grandidens* is most closely related to *P. holthuisi* Bruce, 1969, with which it shares most of the characters presented in the Diagnosis. It differs most noticeably from *P. holthuisi* in its more robust second pereiopod chelae, with the stout teeth along the cutting edges of the fingers, with the carpus about 0.6 of the chela length. In *P. holthuisi* these chelae are more slender, with the carpus generally about subequal to the palm length, and the fingers subequal to the palm length, bearing only few weak teeth on the proximal half of the cutting edges. In *P. grandidens* the ambulatory propods are armed with short spines, in contrast to *P. holthuisi*, and the dactyl bears only a small short accessory tooth, whereas *P. holthuisi* has a well developed tooth about half the length of the unguis. *Periclimenes holthuisi* has a very small *bec ocellaire* (Bruce, 1982a), similar to *P. grandidens*.

ETYMOLOGY. Latin *grandis*, large and *dens*, tooth; a reference to the dentition of the second pereiopods.

REMARKS. The description of *P. grandidens* increases to 11 the number of species in the *holthuisi*-species group. These may now be identified with the following key.

## A KEY TO THE SPECIES OF THE *PERICLIMENES HOLTHUISI*-GROUP

1. Ambulatory dactyls biunguiculate . . . . . 2

Ambulatory dactyls simple; R. 1+7-10/2 . . . . . *P. tosaensis* Kubo, 1951

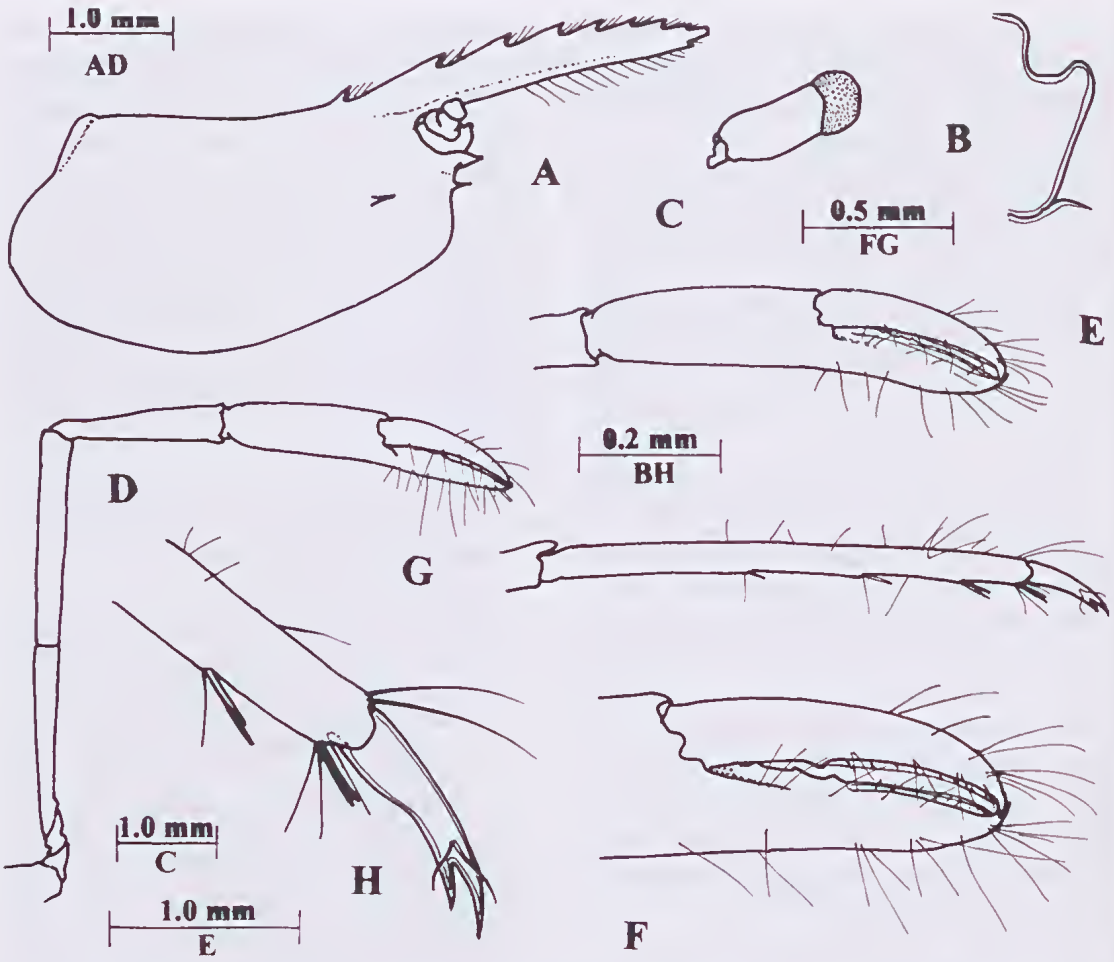


FIG. 11. *Periclimenes* aff. *holthuisi* Bruce, ♂, Milne Bay. A, carapace and rostrum. B, ophthalmic somite, right lateral. C, eyestalk. D, second pereiopod. E, same, chela. F, same, fingers. G, third pereiopod, propod and dactyl. H, same, distal propod and dactyl.

2. Carapace with 2-3 postorbital teeth; R. 2-3 + 6-7/2-4 . . . . . *P. aesopius* (Bate, 1863)

Carapace with 0-1 postorbital teeth . . . . . 3

3. Carapace without postorbital rostral teeth; carpus of second pereiopod longer than chela; R. 5-6/0-2 . . . . . *P. longicarpus* Bruce & Svoboda, 1983

Carapace with postorbital rostral tooth . . . . . 4

4. Rostrum slender; third abdominal tergum posterodorsally subcarinate . . . . . 5

Rostrum with deeper lamina, arched; third abdominal tergum postero-dorsally produced, not markedly carinate . . . . . 6

5. Rostrum straight, upwardly directed, exceeding distal margin of proximal segment of antennular peduncle; first pereiopods with dactylus longer than palm; R. 1+6-7/2-3 . . . . . *P. tenuirostris* Bruce, 1991

Rostrum curved, horizontal, not exceeding distal margin of proximal segment of antennular peduncle; first pereiopods with dactylus shorter than palm; R. 1+6-8/1-3. . . . *P. kobayashii* Okuno & Nomura, 2002

6. Second pereiopod chela with fingers bearing series (5-7) of small acute recurved denticles along both cutting edges 7

Fingers of second pereiopods with few (1-4) larger, acute, proximal teeth . . . . . 8

7. Maxilla with simple distal endite; second pereiopods overreaching scaphocerite by distal part of merus; cutting edges of fingers usually with 6-8 small acute recurved teeth; with well developed *bâc ocellaire*; R. 1+5-7/0-2 . . . . . *P. venustus* Bruce, 1990e

Maxilla with bilobed distal endite; second pereiopods overreaching scaphocerite by proximal part of palm; cutting edges of fingers with 2-4 acute recurved teeth;

with small *bec ocellaire*; R. 1+7-9/1-2 . . . . . *P. sarasvati* Okuno, 2002

8. Second pereiopods with chelae bowed; ophthalmic somite without *bec ocellaire*; R. 1+7-8/1-2 . . *P. magnificus* Bruce, 1979. . . . . Second pereiopods with chelae not bowed, ophthalmic somite with *bec ocellaire* . . . . . 9

9. Third pereiopod dactyl 7 or more times longer than basal width, about 0.28 of propod length, with very slender adpressed accessory tooth; R 0-1+11-13/1 . . . . . *P. adularans* Bruce, 2003

Third pereiopod dactyl 4 times longer than basal width, about 0.2 of propod length, without adpressed accessory tooth . . . . . 10

10. Second pereiopod with carpus subequal to palm length; fingers with 1-6 small teeth; third pereiopod with long spines, dactyl with well developed accessory tooth R. 1+10-13/2-4 . . . . . *P. holthuisi* Bruce, 1969

Second pereiopod with carpus 0.75 of palm length, fingers with 4 large acute teeth, third pereiopod with short spines, dactyl with small accessory tooth; R. 1+8-9/2-3 . . . . . *P. grandidens* sp. nov.

The shrimps referred to *Periclimenes tosaensis* by Debelius (1999: 177) from Milne Bay, (PNG), Ambon, (Indonesia) and Cabilao (Philippines), show the same colour pattern as *P. grandidens* and are possibly conspecific.

The species of the *holthuisi*-group are now well known for their conspicuous species specific colour patterns which make them favourite subjects for underwater photographers. A key to the colour patterns of most species has been provided by Okuno (2002). The colour patterns of some species (*P. adularans, P. tenuirostris*) are still unknown. *Periclimenes grandidens* has a pattern quite distinct from its nearest relative, *P. holthuisi*. The third abdominal tergite in *P. grandidens* has a broadly U-shaped patch, with the arms directed anteriorly, with inner patches of white surrounded, somewhat irregularly, by deep blue patches, outlined narrowly by a fine white border, quite distinct from the white chevron-shaped patch present in *P. holthuisi*, with a bright red anterior border.

The colouration of *P. grandidens* is more similar to *P. sarasvati*, also an associate of a scleractinian coral, *Euphyllia ancora* Veron and Pichon. Okuno (2002) describes the dorsal third abdominal somite as "with white small patch bordered anteriorly and posteriorly by similar sized, purple narrow patches; in dorsal view, anterior patch V-shaped". In addition to the characters listed in the above key, *P. sarasvati* differs in some further small characters that help to distinguish it from *P. grandidens*, in particular the third pereiopod propod bears only a single short, rather robust distoventral spine, with a single similar preterminal ventral spine, *P. grandidens* has a pair of short slender distoventral spines and three further spines along the ventral margin; also the dactylar accessory tooth is about half the length of the unguis in *P. sarasvati*, but only about 0.12 of the unguis length in *P. grandidens*; the dactylus is also more slender, about 4.5 times longer than the basal width, about 3.6 times in *P. grandidens*.

The strongly produced acute inferior orbital angle is one of the major characters of the *holthuisi*-species group, with its characteristic ventral flange. Okuno (2002) has commented on a "small raised lobe" on the dorsum of the basicerite in *P. sarasvati*, an acute process in *P. grandidens*. The proximal dorsolateral process of the proximal segment of the antennal peduncle present in *P. grandidens* is not mentioned in Okuno's description but is shown in his Figure 1. These features all appear to form part of a complex of related morphological characters and are likely to be present in other species of this group.

### **Periclimenes** aff. **holthuisi** Bruce, 1969 (Figs 11, 22D)

*Periclimenes holthuisi* Bruce, 1969: 258; 1982: 244, fig. 7; Fransen, 1989: 139, figs 4a, 5ab, 6a-f, 7a-g; De Grave, 2000:136; Li, 2000: 190, fig. 241; Davie, 2002: 327.

MATERIAL. 1 ♂, AMPI 1371, Milne Bay, 12 m, 16 November 2002, QMW27241.

DIAGNOSIS. Rostrum subequal to CL, dentition 1+7/1, elevated, at about 15°, not arched (Fig. 11A); antennal spine acutely produced with small ventral flange, largely concealed by anterior margin of carapace; third abdominal tergite non-carinate; ophthalmic somite with small blunt tubercle (Fig. 11B), eyestalk elongate, greater than half CL, (Fig. 11C), cornea globular, poorly pigmented, about 0.25 of CL; second pereiopods (Fig. 11D), subequal, chelae (Fig. 11E), not bowed, fingers (Fig. 11F), subequal to palm length, dactyl with single small acute tooth, fixed finger with three small acute teeth proximally, with numerous long setae, carpus 1.3 times palm length; ambulatory pereiopod dactyls (Fig. 11H), about 4.5 times longer than proximal width, 0.2 of propod length, biunguiculate, accessory tooth well developed, not adpressed, propods (Fig. 11G), with well developed paired distoventral and distal ventral spines, with two shorter ventral spines.

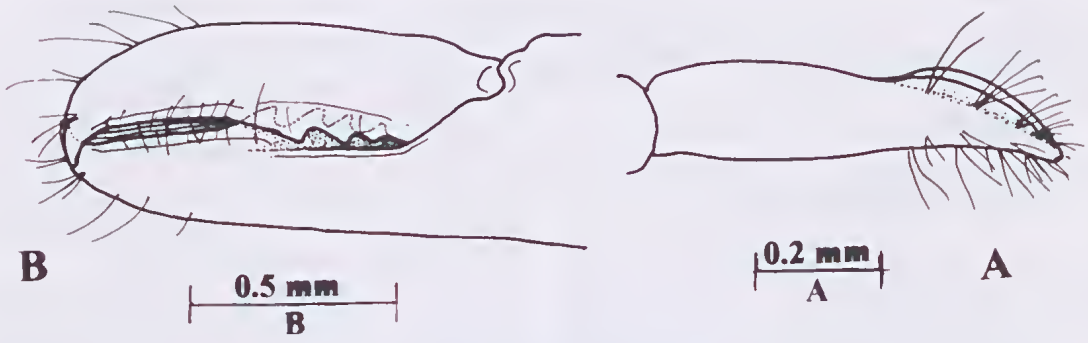


FIG. 12. *Periclimenes inornatus* Kemp. A, first pereiopod chela. B, fingers of major second perciopod.

DESCRIPTION. Closely similar to *Periclimenes holthuisi*. The specimen has a CL of 2.8 mm, and has a rostral dentition of 1+ 7/1 (Fig. 20A), with the rostrum directed dorsally, with the tip of the rostrum missing. Utilising the characters provided in the key to the *P. holthuisi*-group provided above, the specimen has a less strongly dentate rostrum (1+10-13/2-4 in *P. holthuisi*), with only a very small tubercular *bée ocellaire*, which also contrasts with *P. holthuisi*, and has the fingers of the second pereiopod chelae less strongly armed, with one dactylar and three small teeth on the fixed finger, rather than two and four as reported by Bruce & Svoboda (1983). A single tooth only is present on each finger in the type material. The reference to *P. holthuisi* in Bruce & Svoboda, 1983 is erroneous. The material referred to, was incorrectly identified and is being described separately as a new species.

HOST. *Megalactis hemprichii* Ehrenberg, 1834 [Actininaria] (Karen Gowlett-Homes, pers. comm., 10 October 2003).

COLOURATION (From colour transpareney, AMPI 1371). Mainly transparent. Rostrum, seaphoeerite, flagella and ambulatory pereiopods colourless. Third abdominal segment with conspicuous posterodorsal patch, consisting of a red eresecnt posteriorly, a central white zone , with white median and lateral lobes with blue distal areas. Ventral abdomen with sparse red and white dots. Posterior margin of sixth abdominal segment reddish, also protopod of uropod, rami distally white. Cornea white. Second pereiopods with palm white, fingers blue, carpus white proximally, blue distally.

REMARKS. The colour pattern does not correspond to that of *P. holthuisi* s.str. The morphological differences from *P. holthuisi* s. str., and the association with *Megalactis hemprichii*, suggest that this specimen represents an undescribed taxon. As it may be immature, and no adult females are available, it is preferable to await the collection of further material before adding to the already complex *P. holthuisi*-species group.

The specimen also shows some resemblance to the specimen from the Spermonde Archipelago reported on by Fransen (1989, as *P.* aff. *holthuisi*, associated with an anemone, *Actinodendron* sp.) but differs from this specimen in having a less arched rostrum, more weakly dentate fingers on the second pereiopods and a less distinct, blunt bée ocellaire. The dorsal telson spines are also larger and at about 0.5 and 0.75 of the telson length, not minute at 0.65 and 0.82.

*Periclimenes holthuisi* has been reported in association with numerous coelenterates, reviewed by Fransen (1989): *Dofleinia armata* Wassillief, *Entacmaea quadricolor* (Rüppell), *Heteractis* sp., and *Radianthus ritteri* (Kwietniewski) (Actinaria), together with the fungiid coral *Heliofungia actiniformis* (Quoy & Gaimard), and the scyphozoan *Cassiopea andromeda* (Forskål). It has not been reported in association with *Megalactis* spp. A specimen, *P.* cf. *holthuisi*, was reported in association with an anemone, *Actinodendron* sp., by Fransen (1989). Bruce & Svoboda (1984) list several actinarians and scleractinians as hosts for this species. However, this was compiled before many of the species in this group had been described and probably many records need confirmation.

DISTRIBUTION. PNG – Kranket Island, Madang, 36 m (Bruce, 1976b), Loloata Island (Coleman, 1998) and Duangit reef, Hansa Bay, 20 m (De Grave, 2000). Other – Type locality: Lung Ha Wan, Hong Kong. Recorded also from Jordan, Zanzibar, Maldive Islands, Sri Lanka,

Malaya, Singapore, Indonesia, Vietnam, China, Hong Kong, South China Sea, Japan, Philippines, Northern Territory, Queensland, New Caledonia, Caroline Islands, and Marshall Islands.

### Periclimenes incertus Borradaile, 1915

*Periclimenes (Cristiger) incertus* Borradaile, 1915: 210; 1917: 364, pl. 53 fig. 7.
*Periclimenes (Periclimenes) impar* Kemp, 1922: 147, figs 16-17, pl. 3 fig. 1.
*Periclimenes (Periclimenes) incertus*; Holthuis, 1959: 193.
*Periclimenes incertus*; Li, 2000: 193, fig. 244; Davie, 2002: 327.

MATERIAL. 1 ♂, 1 ov. ♀, AMPI—, # 33, Loloata Island, 8 m, 11 April 2003, QM W27240.

HOST. *Oceanapia* sp. (Phloeodictyidae, Porifera).

COLOURATION. No data.

REMARKS. Often found with *Thanmastocaris streptopus*. The specimens present no special features. Both specimens show the characteristic robust ambulatory dactyl, with a large stout accessory tooth. The male has a rostral dentition of 10/2, the female's rostrum is largely missing. The male lacks both second pereiopods. The female has both, the larger with the fingers distinctly gaping distally, as in Holthuis (1952, fig. 7e, as *P. impar*), indicating that this feature may occur in both sexes. The association with *Oceanapia* represents a new host record.

DISTRIBUTION. PNG – Davit Wreck; Sushi Maru Wreck, Laing Island, Hansa Bay, from 9-11 m in sponges (De Grave, 2000). Other – Type locality: South Nilandu Atoll, Maldive Islands. Recorded from the Yemen, Kenya, Zanzibar, Tanganyika, Madagascar, Maldive Islands, Sri Lanka, Andaman Islands, Singapore, Indonesia, Philippines; Western Australia, Northern Territory, Queensland, and New Caledonia,.

### Periclimenes inornatus Kemp, 1922 (Fig. 12)

*Periclimenes (Ancylocaris) inornatus* Kemp, 1922: 191, figs 44-46.
*Periclimenes inornatus*; Bruce, 1976a:103, figs 10-11; Li, 2000: 196, fig. 248; Jayandran 2001: 203, fig. 86; Davie, 2002: 328.

MATERIAL. (1) 1 ♂, AMPI 1456, #143, Loloata Island, 16 m, 24 April 2003, QMW27242. (2) 1 ♂, AMPI, # 144, Loloata Island, 24 April 2003, QM W27243.

HOST. (1) *Stichodactyla mertensii* Brandt. (2) Specimen found with *M. psamathe* (?), see above.

REMARKS. Rostral dentition 7-8/1. Specimen (2) with fourth thoracic sternite with well developed transverse ridge with open median notch. First pereiopod chela (Fig. 12A) with fingers broadly expanded laterally, with entire lateral cutting edges, with small acute articulated tips. Second pereiopods subequal, chela about 0.6 of CL, fingers (Fig.12 B) about 0.6 of palm length, with three well developed stout acute slightly recurved teeth on the dactylus, four similar teeth on the fixed finger, the dactylar teeth opposing inside the fixed finger teeth. Third ambulatory dactyl with non-spinulose unguis.

COLOURATION (From colour transparency, AMPI). Semi-transparent, with pinkish tinge, without conspicuous colouration, white chromatophores along dorsal eyestalk and along thoracic gut.

DISTRIBUTION. PNG– Hansa Bay, Laing Island; Davit Wreck; Wanginam reef; Bisal Paap reef; 6-30 m; on *Actinodendron plumosum; Heteractis magnifica* (De Grave, 2000). Other – Type locality: Great Cocos Island, Port Blair, Andaman Islands. Known from Kenya, Zanzibar, Comoro Islands, Seychelle Islands, Maldive Islands, Andaman Islands, Indonesia, South China Sea, Japan; Western Australia, Queensland, Solomon Islands, Caroline Islands, and Fijian Islands.

### Periclimenes magnificus Bruce, 1979

*Periclimenes magnificus* Bruce, 1979: 195, figs 1-5, pl. 1a-c; Li, 2000:212, fig. 274.

MATERIAL. 1 spm, ?♂, AMPI ??, Loloata Island, April 2003.

HOST. *Cassiopea* sp. [Scyphozoa].

COLOURATION (From colour transparency, AMPI ?). Corneae, eyestalks, antennal peduncles, second pereiopods white; carapace with poorly developed transverse white patch, larger more distinct white posterodorsal patch on third abdominal tergite, small white median dots on fourth and fifth segments, second pereiopod finger tips blue, caudal fan largely white with conspicuous blue dot on distal uropodal endopod.

REMARKS. Specimen not collected. Data from colour transparency. The colouration is consistent with being a male. The third abdominal segment dorsal patch lacks the red anterior margin conspicuous in the female (Bruce, 1980a: 41). This species has not been reported in association with scyphozoans. Previously associated with actinarians, *Dofleinia armata* Wassilieff, 1908, and *Radianthus cooki* (Verrill); scleractinians, *Cataphyllia jardinei* (Saville-Kent), *Fungia armata* (Alcock), and alcyonarians, *Lobophyton* sp. (Bruce & Svoboda, 1983; Fransen, 1989; Nomura, 1989;

Debelius, 1999). Debelius's photo (1999: 181) suggests that the species may be a fish cleaner.

DISTRIBUTION. PNG– Loloata Island (Coleman, 1998). Rabaul [*P.* sp., cf. *magnificus*] (Debelius, 1999). Other – Type locality: Wistari Reef, Capricorn Islands, Queensland. Known also from Thailand, Indonesia, Japan, Philippine Islands, Northern Territory, Queensland, and New Caledonia.

### Periclimenes soror Nobili, 1904

*Periclimenes soror* Nobili, 1904: 232; Bruce, 1978a; 299, figs 1-6; Li, 2000: 237, fig. 316; Davie, 2002: 332.
*Periclimenes (Periclimenes) soror*; Holthuis, 1952: 51, fig. 17.

MATERIAL. 2 ovig. ♀, AMPI 1435, # 66, Loloata Island, 10 m, 17 April 2003, QM W27234.

HOST. *Protoreaster nodosus*. (Linn.) [Echinodermata: Asteroidea].

COLOURATION (From colour transparency, AMPI 1435). Uniform deep red.

REMARKS. The specimens present no special features: rostral dentition 11/0.

DISTRIBUTION. PNG – New Britain and Bougainville (Bruce, 1978); Loloata Island (Coleman, 1998); Port Moresby, Kimber Bay, (*Bicolor* form, on *Acanthaster*) (Coleman, 2000); Awar; Duangit; Laing Island, Hansa Bay; 3-10 m; on *Linckia guildingi, Choriaster granulatus,* and *Culcita novaeguineae* (De Grave, 2000). Other – Type locality: Jibuti. Also reported from Saudi Arabia, Kenya, Zanzibar, Tanganyika, Madagascar, Seychelle Islands, Chagos Islands, Sri Lanka, Malaya, Indonesia, Vietnam, China, Hong Kong, Taiwan, Japan, Philippines, Sabah, Bismarck Archipelago, Solomon Islands, Western Australia, Northern Territory, Queensland, New South Wales, Lord Howe Island, New Caledonia, Marshall Islands, Mariannas Islands, Fijian Islands, Hawaiian Islands, Society Islands, Tuamotu Islands. Also Mexico, Panama, Colombia.

### Periclimenes venustus Bruce, 1990a

*Periclimenes venustus* Bruce, 1990a: 230, figs 1-6, 7a, 8a; De Grave, 1998b: 16, fig. 1; 2000: 140; Li, 2000: 246, fig. 327; Davie, 2002: 333.

MATERIAL. (1) 1♂, 1 ov. ♀, AMPI 1373, Milne Bay, 18 m, November 2002, QM W27237; (2) 1 ov. ♀, AMPI 1451, # 38, Loloata Island, 8 m, 11 April 2003, QM W27236; (3) 1 ovig. ♀, AMPI 1447, # 78, Loloata Island, 15 m, 18 April 2003, QM W27235. (4) 1 juv.♀, AMPI 1350, Loloata Island, 15m, November 2001, QM W25873.

HOST. (1) (2) (3), *Heliofungia actiniformis* Quoy and Gaimard [Fungiidae]. (4) unidentified anemones.

COLOURATION (From colour transparency, AMPI 1373). (1) Female: Body mainly transparent; carapace with broad transverse white mid-dorsal patch, with four sets of paired blue and white chromatophores close to posterior margin, with similar white-blue-white groups along lower branchiostegite; third abdominal segment with cordiform posterodorsal white patch, apex posteriorly, colour most intense along outer border, with submedian blue dots anteriorly, similar, more widely separated pair posteriorly; proximal caudal fan heavily spotted with blue and white chromatophores, centrally colourless, distal exopod largely white with large dark blue terminal patch, endopod with several small white dots, posteriorly blue, telson tip similar; antennular peduncle sparsely dotted with white and blue; antenna colourless; eyestalk with blue-white dots; mouthparts colourless; second pereiopods with articulations and distal third of fingers deep blue, proximal two thirds of fingers, palm, carpus and distal merus and ischium heavily spotted with coarse white dots; first pereiopods similar but colouration less strong; ambulatory pereiopods transparent; pleopods heavily spotted with blue and white. Male: Similar to female but pattern less strongly developed, without transverse white patch on carapace, white abdominal patch feebly developed but two pairs of blue spots distinct; second pereiopods similar to female. (From colour transparency, AMPI 1451) (2) Ovigerous female: Generally similar to (1) but without a transverse dorsal patch on the carapace and the posterodorsal third abdominal tergite with a large sub-cordiform patch of pink, with a star shaped central transparent area, internal and external margins of patch white. (4) Juvenile female, generally consistent colouration, but with dorsal abdominal patch less distinctly developed.

REMARKS. Rostral dentitions: (1) male, 7/1; female 8/2, distalmost teeth minute; (2) 7/1: (3) 9/2; (4) 8/1. *Bec ocellaire* well developed, angular, subacute. The colouration agrees closely with that of the type material. The dentition of the second perciopod fingers is (L,R; dactyl/fixed finger) (1) 4/6, 4/4; 4/7, 4/7; (2) 5/8,4/7; (3) 7/7, 6/8; (4) 3/6,-/-. Range of finger dentition 4-7/4-8, all teeth small, generally slightly recurved.

DISTRIBUTION. PNG – Loloata Island (Coleman, 1998); Laing Island, Hansa Bay, 5-30 m, (De Grave, 1998b; 2000). Other – Type locality: Port Essington, Northern Territory. Known also from Indonesia, Japan, Philippine Islands, Western Australia, Northern Territory, Queensland, Lord Howe Island, and (??) Micronesia.

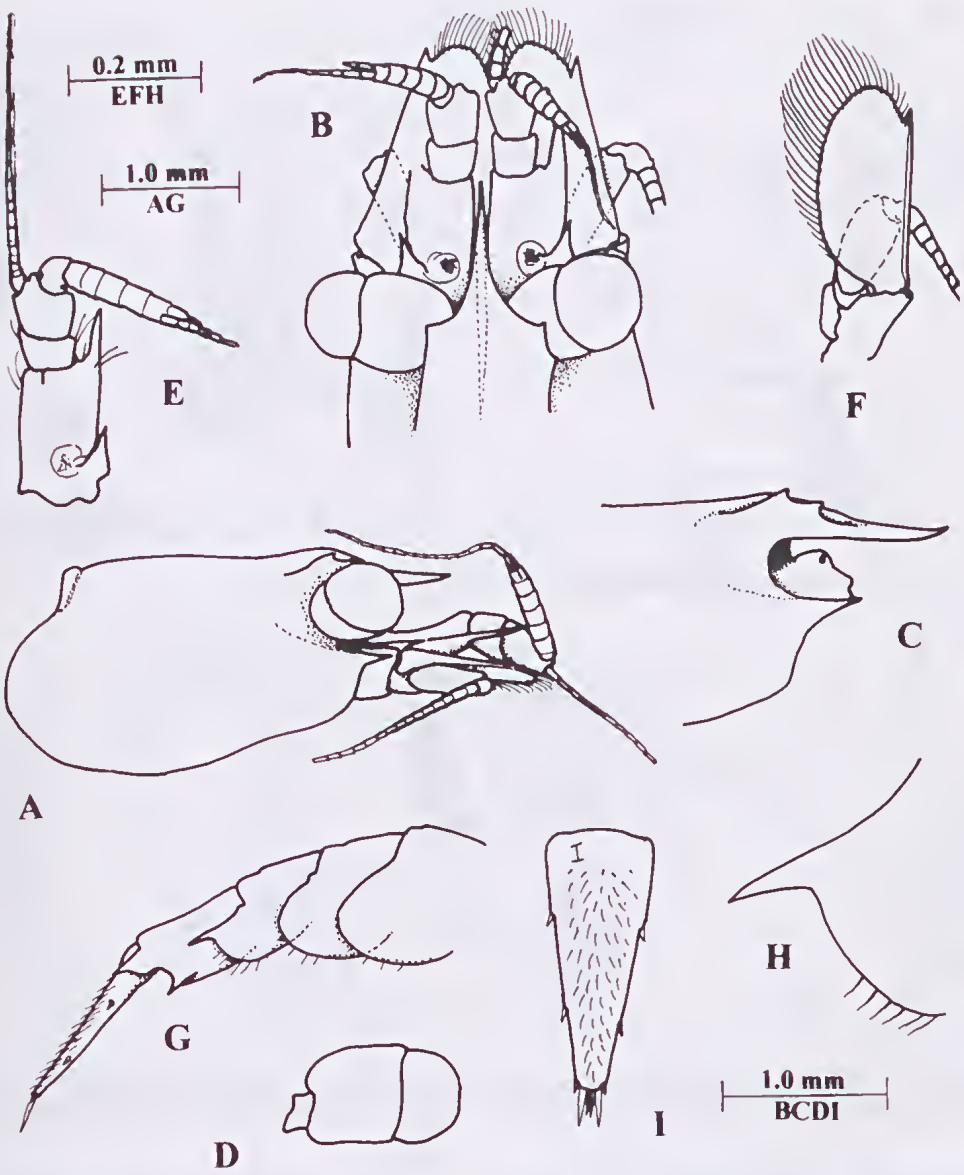


FIG. 13. *Pontonides asperulatus* sp. nov., holotype ♀. A, carapace and antennae, lateral. B, anterior carapace and antennae, dorsal. C, anterior carapace and rostrum. D, eye. E, antennule. F, antenna. G, posterior abdomen and telson. H, fifth abdominal segment, pleuron. I, telson.

**Pontonides asperulatus** sp. nov.
(Figs 13-16, 22E)

MATERIAL. 1 ♀, holotype, AMPI1455, # 116, Horseshoe Reef, Loloata Island, 16 m, 22 April 2003, QMW27227.

DIAGNOSIS. Supraorbital carina angular, unior bidentate, carapace and abdomen smooth, eyestalk without dorsal tubercle, third maxilliped with fusiform setae laterally on basal region of exopod, with rudimentary arthrobranch, fingers of first pereiopod chela with cutting edges denticulate, second pereiopods grossly unequal, dissimilar, major chela densely setose and tuberculate, fingers with cutting edges coarsely dentate, abdomen with fifth segment pleuron strongly posteroventrally produced, telson dorsally densely setose, with flattened fusiform setae.

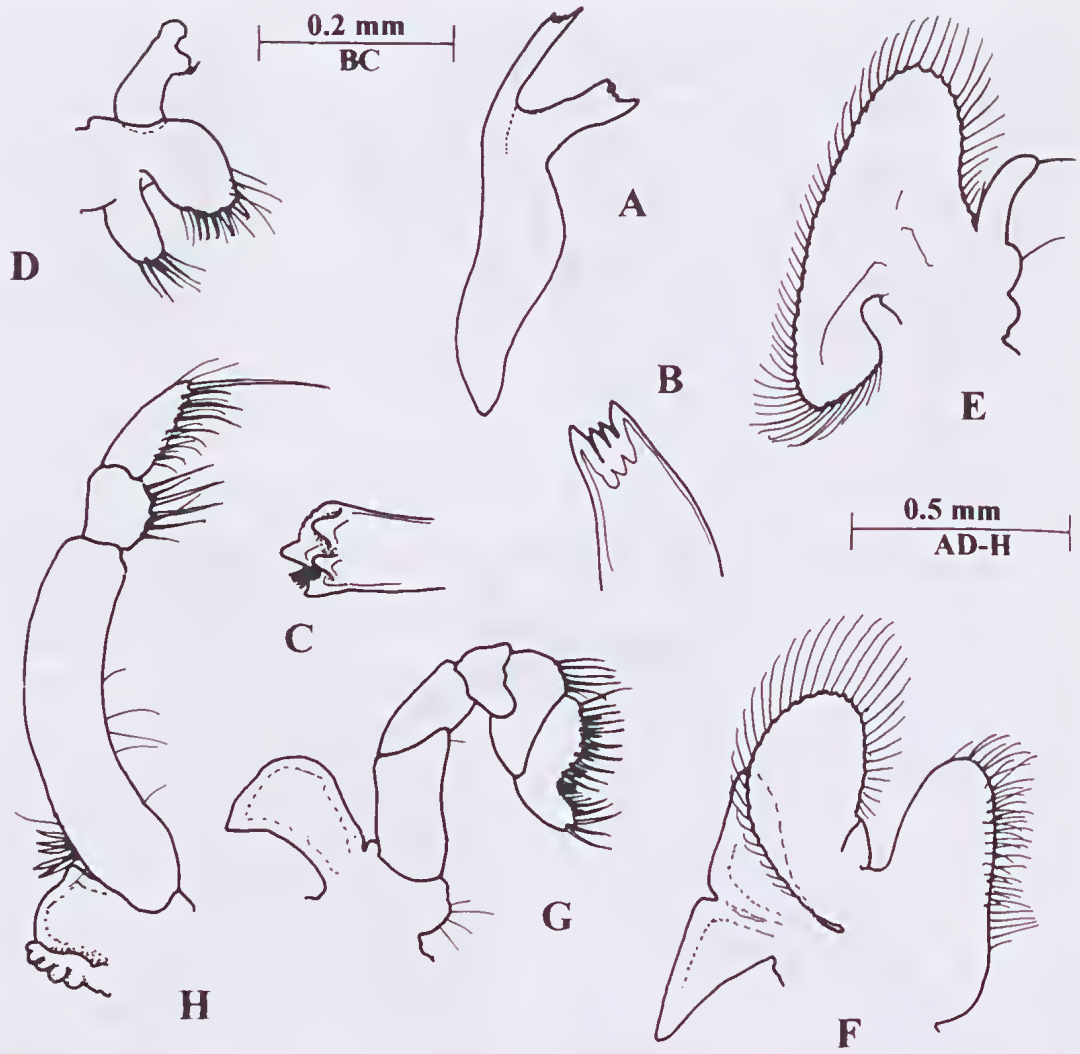


FIG. 14. *Pontonides asperulatus* sp. nov., holotype ♀. A, mandible. B, same, incisor process. C, same molar process. D, maxillula. E, maxilla. F, first maxilliped. G, second maxilliped. H, third maxilliped.

DESCRIPTION. Body form small, subcylindrical, slightly depressed.

Carapace (Fig. 13A) and abdomen smooth, non-areolate, glabrous. Rostrum slender, oval in section distally, unarmed, slightly up-curved distally, reaching to near distal end of proximal segment of antennular peduncle, lateral carinae obsolete on distal third, broadly expanded over bases of eyestalks (Fig. 13B), angular, with one small lateral angle on left and two on right, orbit (Fig. 13C) well developed, inferior orbital angle broadly convex, antennal spine very well developed, reaching almost to distal margin of basicerite, without epigastric, hepatic or branchiostegal spines, anterolateral angle broadly convex.

Abdomen (Fig. 13G) with third abdominal segment not posterodorsally produced, sixth segment about 1.7 times longer than deep, 1.23 times fifth (Fig. 13H) segment length, 0.44 of CL, posterolateral angle large and very acute, posteroventral angle acute, smaller, pleura of first four segments broadly rounded, fifth posteriorly produced, with very large slender acute tooth at posterodorsal angle.

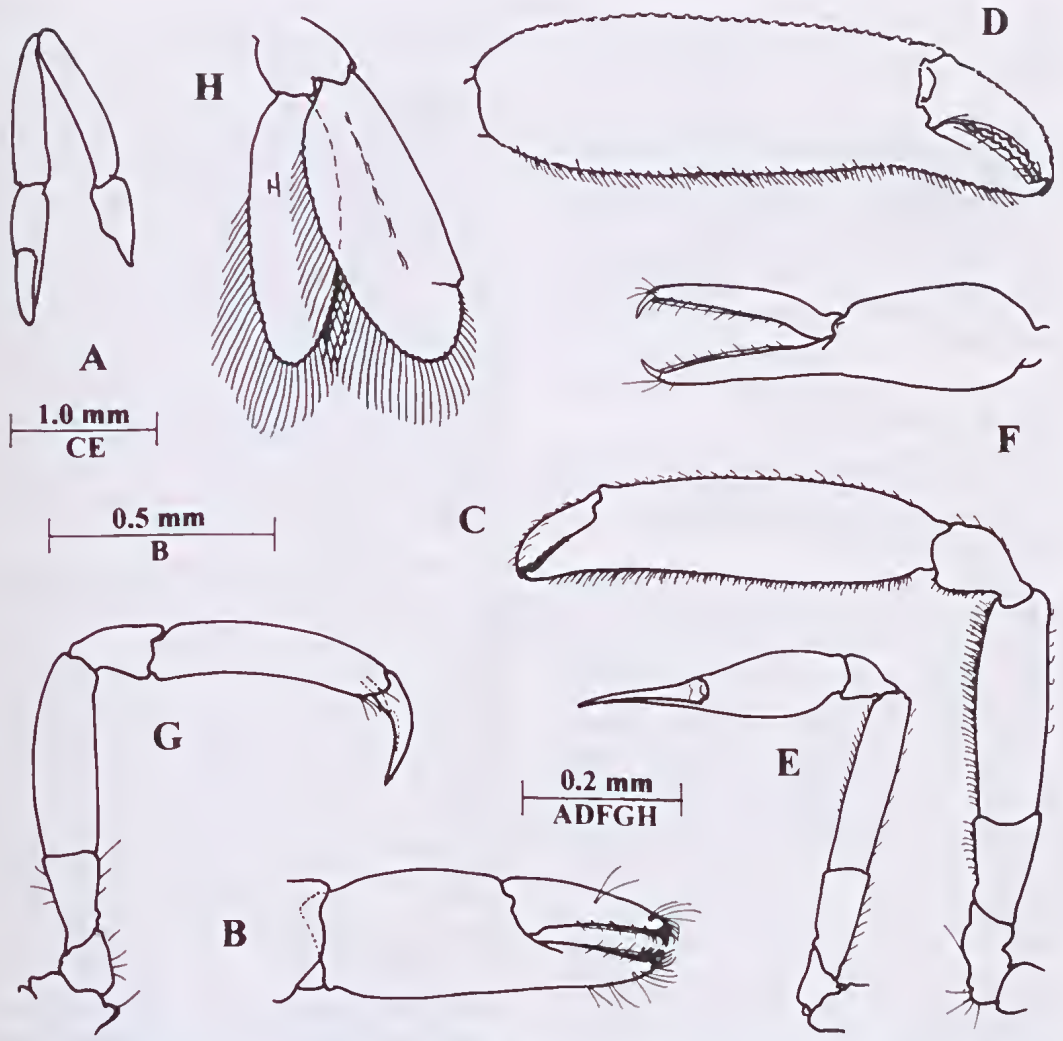


FIG. 15. *Pontonides asperulatus* sp. nov., holotype ♀. A, first pereiopod. B, same, chela. C, major second pereiopod. D, same, chela. E, minor second pereiopod. F, same, chela. G, third pereiopod. H, uropod.

Telson (Fig. 13I) length about 0.77 of CL, 1.7 times sixth abdominal segment length, 2.4 times longer than anterior width, with two pairs of small lateral marginal dorsal spines at about 0.38 and 0.75 of telson length, posterior margin about 0.28 of anterior width, rounded, without median point (Fig. 16I), with small lateral spines subequal to dorsal spines, intermediate spines robust, about 0.14 of telson length, submedian spines slender, setulose, about 0.6 of intermediate spine length, dorsal surface with numerous short fusiform setae (Fig. 16J).

Antennule (Fig. 13E) with proximal segment of pedunele parallel sided, about 1.7 times longer than wide, with anterolateral angle (Fig. 16A) (damaged on left side) very strongly produced, acute, reaching to middle of distal segment of pedunele, anterolateral lobe very small, convex, with single plumose seta, styloeerite short, acute, reaching to about 0.5 of segment length, without ventromedial tooth; intermediate and distal segments short and stout, combined length about 0.7 of proximal segment length; upper flagellum proximally stout, biramous, with five proximal

segments fused, shorter free ramus with two segments, longer ramus filiform, with about 17 segments, with about 12 groups of aesthetascs.

Antenna (Fig. 13F) with stout unarmed basiecrite; carpocerite about twice as long as wide, flattened, exceeding proximal segment of antennular peduncle; flagellum well developed; scaphocerite exceeding antennular peduncle, lamina broad, about 2.2 times longer than width, lateral margin straight, with small distolateral tooth at 0.83 of lamellar length, well exceeded by distal lamina.

Ophthalmic somite without *bec ocellaire*, with small black pigment spot.

Eye (Fig. 13D) wel-developed, with hemispherical cornea, without accessory pigment spot, diameter subequal to stalk length, stalk without dorsal tubercle.

Mandible (Fig. 14A) without palp, molar process (Fig. 14C) robust, distally truncate, with five blunt teeth, with small bunch of short setae posteriorly, incisor process (Fig. 14B) slender, with four distal teeth, central pair smaller than outer pair. Maxillula (Fig. 14D) with distinctly bilobed palp (Fig. 16B), upper lobe non-setose, lower lobe with small tubercle with single, short simple seta, upper lacinia broad with five short simple spines distally and numerous longer setae, lower lacinia with setae only. Maxilla (Fig. 14E) with well developed palp, curved, blunt, with single short simple terminal seta, basal region convex without distinct endites, with single short simple seta, coxal region similar, without seta. Scaphognathite well developed, about 2.25 times longer than broad. First maxilliped (Fig. 14F) with short pointed non-setose palp (Fig. 16C), basal and coxal endites fused, basal portion with sparse simple setae, coxal region with few setae, exopod with large broad caridean lobe, flagellum reduced to small knob on proximal medial margin, epipod large triangular, bilobed. Second maxilliped (Fig. 14G) with typical endopod with dactylar segment deeply emarginate medially, with numerous robust serrulate spines, without exopod, epipod well developed with acute posterolateral angle, without podobranch. Third maxilliped (Fig. 14H) with robust endopod, reaching to about middle of carpocerite, proximal segment bowed, uniform, about 5.3 times longer than width, sparsely setose, with six fusiform setae laterally on basal region (Fig. 16D), without exopod, lateral plate of coxa anteriorly pointed, with small, poorly lamellate arthrobranch.

Fourth thoracic sternite with broad, subrectangular transverse plate.

First pereiopod (Fig. 15A) slender, exceeding the carpocerite by the carpus and chela; chela (Fig. 15B) with palm moderately compressed, about 1.5 times longer than deep, fingers (Fig. 16E) broad, about 0.9 of chela length, tapering, with well developed articulated terminal spines, surrounded by short stout setae, dactylus (Fig. 16F) about 3.4 times longer than proximal depth, cutting edge lateral, weakly denticulate over distal half, with sharp entire lamella laterally, fixed finger similar, about 3.0 times longer than proximal depth; carpus slightly longer than chela, tapering proximally, about 4.0 times longer than distal width; merus about 1.1 times carpus length, uniform, slightly bowed, 5.6 times longer an wide; ischium 0.5 of merus length; basis typical; coxa with small distoventral lobe.

Second pereiopods well developed, grossly unequal, dissimilar. Major second pereiopod (Fig. 15C) with chela (Fig. 15D) oval in section, 2.8 times longer than central depth, 1.7 times CL, tapering slightly distally, densely covered with minute acute tubercles on lateral surface and short erect simple setae, fingers (Fig. 16G) about 0.35 of palm length, robust, with lateral cutting edges, tips stout, acute, hooked, dactylus about 2.1 times longer than proximal depth, cutting edge coarsely dentate with about 9 blunt teeth, decreasing in size proximally, fixed finger similar, 1.7 times longer than proximal depth, cutting edge similar to dactylus; carpus short, stout, unarmed, about 0.25 of chela length, strongly tapered proximally, about 1.6 times distal width, ventral surface spinulate, setose; merus about 0.66 of palm length, 3.2 times longer than central width, subuniform, unarmed, ventral surface densely spinulate, setulose; ischium 0.5 of merus length, 1.5 times longer than distal width, tapering proximally, ventral surface spinulate, setulose: basis and coxa without special features.

Minor second pereiopod (Fig. 15E) with chela (Fig. 15F) about half major chela length, 1.25 of CL; palm twice as long as proximal depth, tapering strongly distally, smooth, glabrous, fingers long, slender, equal to palm length, compressed, with strongly hooked articulated tips, dactylus about 6.0 times longer than proximal depth, tapering gradually distally, with entire sharp lateral cutting edge, fixed finger similar; carpus short, stout, unarmed, glabrous, non-tuberculate, about 0.4 of palm length; merus

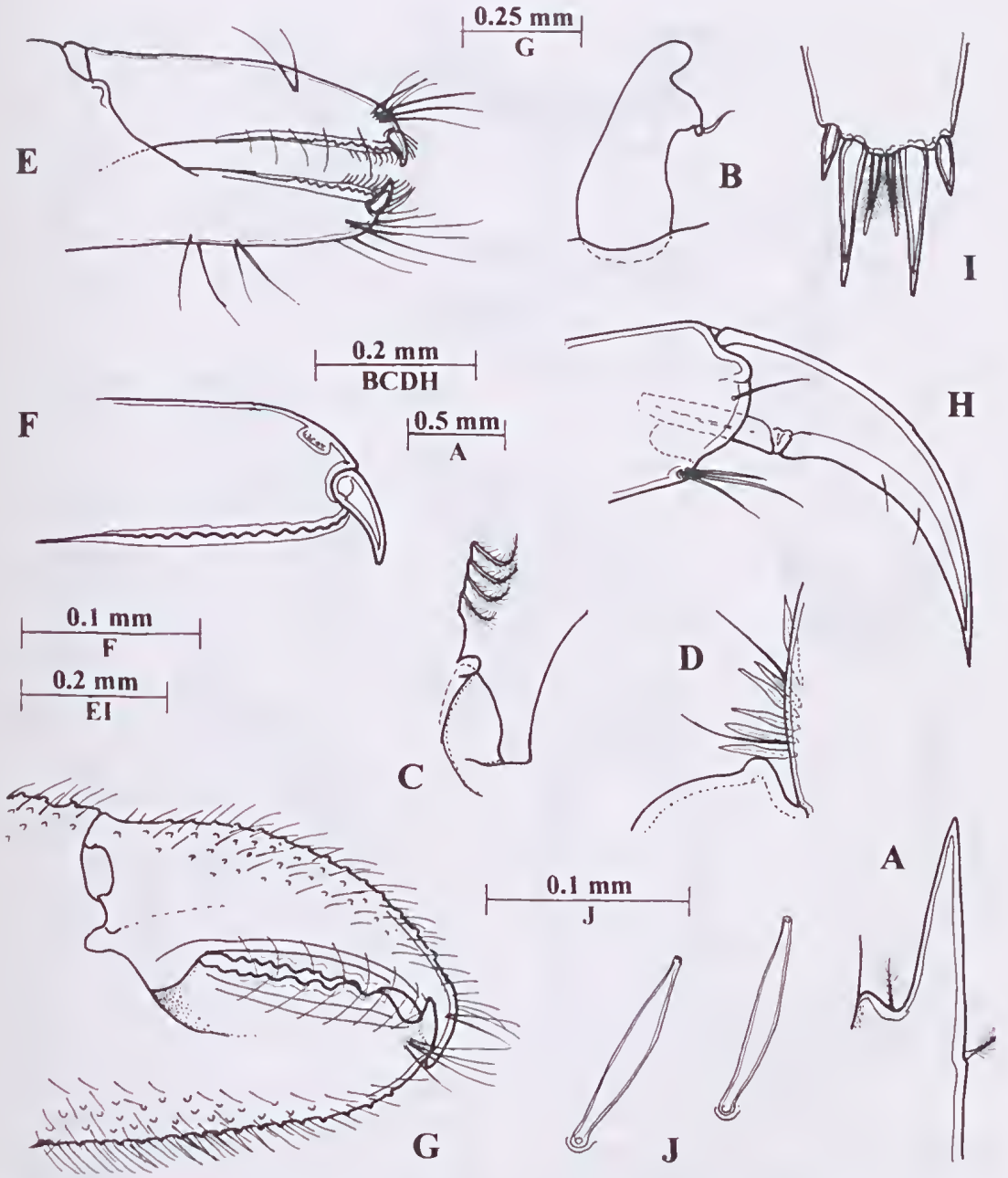


FIG. 16. *Pontonides asperulatus* sp. nov., holotype ♀. A, antennular peduncle, distolateral angle of proximal segment. B, maxillula, palp. C, first maxilliped, palp. D, third maxilliped, proximal region of proximal segment of endopod, lateral aspect. E, first pereiopod, fingers. F, same, distal daetylus. G, major second pereiopod, fingers. H, third pereiopod, distal propod and daetylus. I, telson, posterior spines. J, same, dorsal setae.

1.4 times palm length, unarmed, subuniform, 4.0 times longer than central width, ventrally densely setose; ischium 0.6 of merus length, 2.6 times longer than distal width, moderately tapering

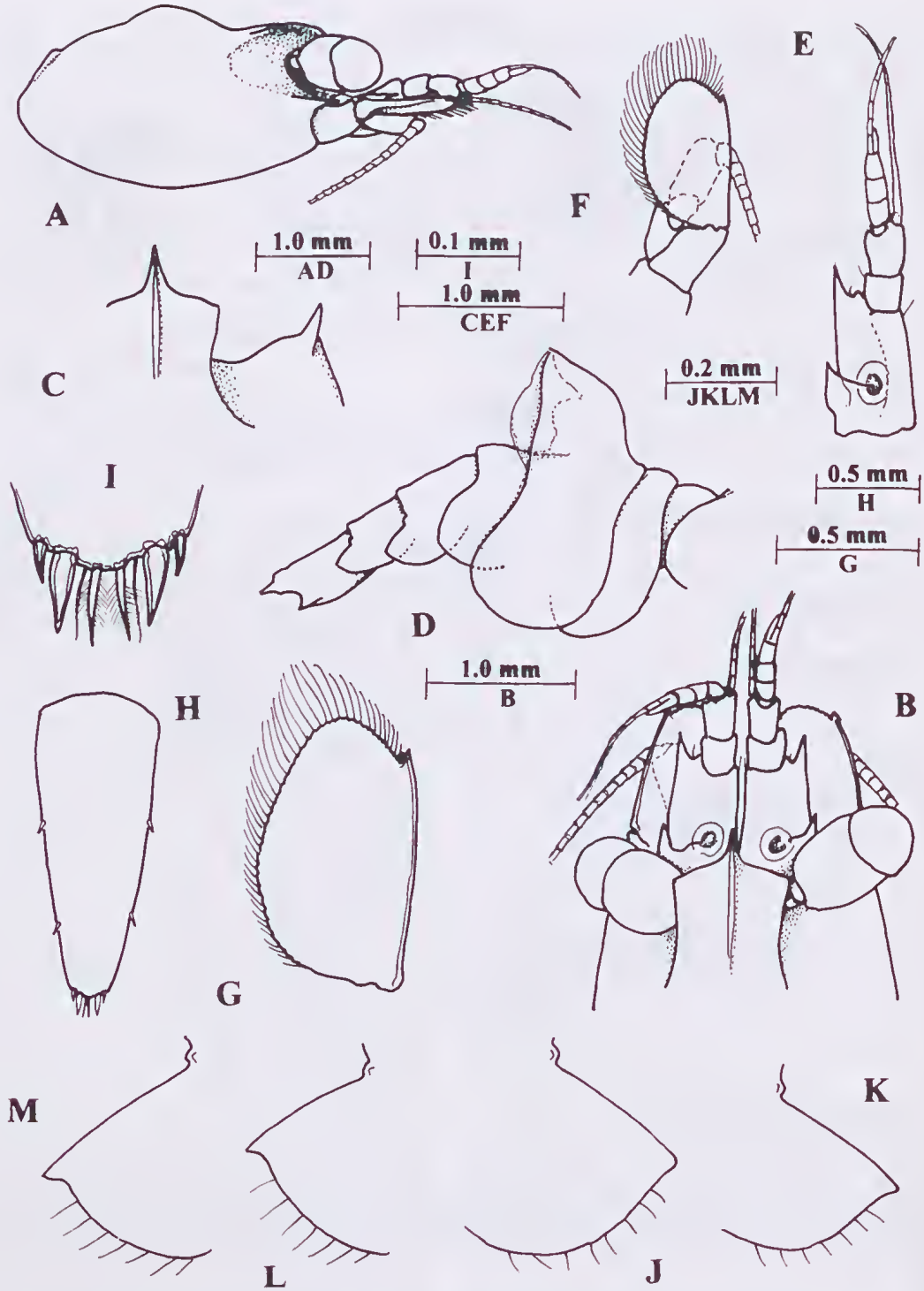


FIG. 17. *Pontonides loloata* sp. nov., paratype ♀. A, carapace and antennae, lateral. B, same, anterior dorsal aspect. C, right orbital region, dorsal. D, abdomen, lateral. E, antennule. F, antenna. G, seaphoecrite. H, telson. I, same, posterior spines. J, K, fourth and fifth pleura, female, left. L, M, same, ♂, right.

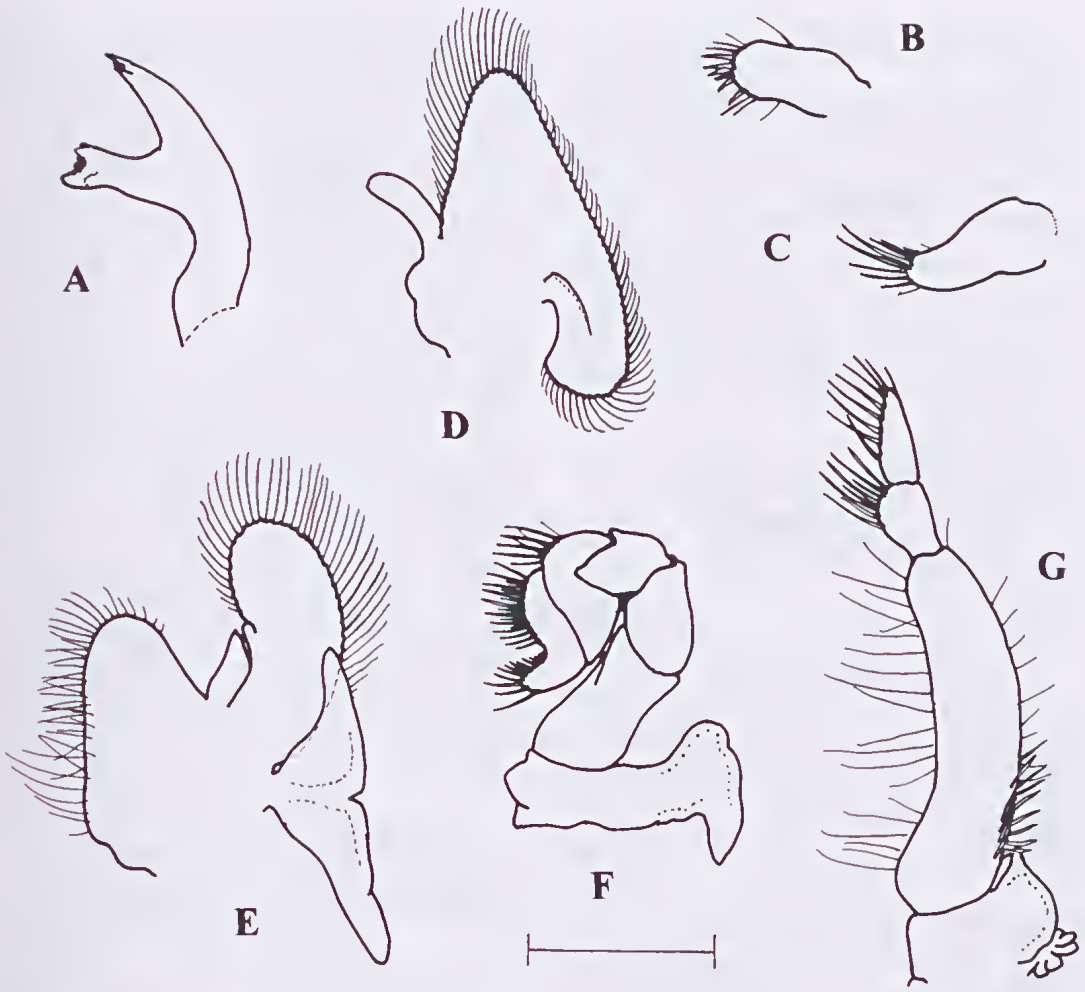


FIG. 18. *Pontonides loloata* sp. nov., paratype ♀. A, mandible. B, maxillula, upper lacinia. C, same, lower lacinia. D, maxilla. E, first maxilliped. F, second maxilliped. G, third maxilliped.

proximally, dorsal margin setose, basis and coxa without special features.

Third pereiopod (Fig. 15G) stout, exceeding carpocerite by about half propodus length,; dactylus (Fig. 16H) large, stout, simple, strongly curved, about 0.5 of propodus length, 4.0 times longer than proximal width, ventral edge sharply carinate, with large basal plate proximally; propodus about 0.6 of CL, bowed, subuniform, 5.0 timed longer than deep, deeply emarginate distoventrally, without spines, with sparse setae distally; carpus short, unarmed, about 0.35 of propodus length1.5 times longer than distal width; merus about 0.84 of propodus length, 3.0 times longer than central width, unarmed; ischium 0.5 of meral length; basis without special features; coxa with small ventral lobe. Fourth and fifth pereiopods similar to third.

Pleopods without special features.

Uropod (Fig. 15H) with protopodite posteriorly unarmed; rami extending well beyond telson: exopod about 2.6 times longer than wide, with two small spinules at posterolateral angle on left, damaged on right, diaeresis weakly developed; endopod about 0.88 of exopod length, 3.0 times longer than wide.

MEASUREMENTS. Holotype ♀, carapace length, 1.75; carapace and rostrum, 2.9; total body length (approx.), 8.0; second pereiopod, major chela, 3.15; minor chela, 2.1.

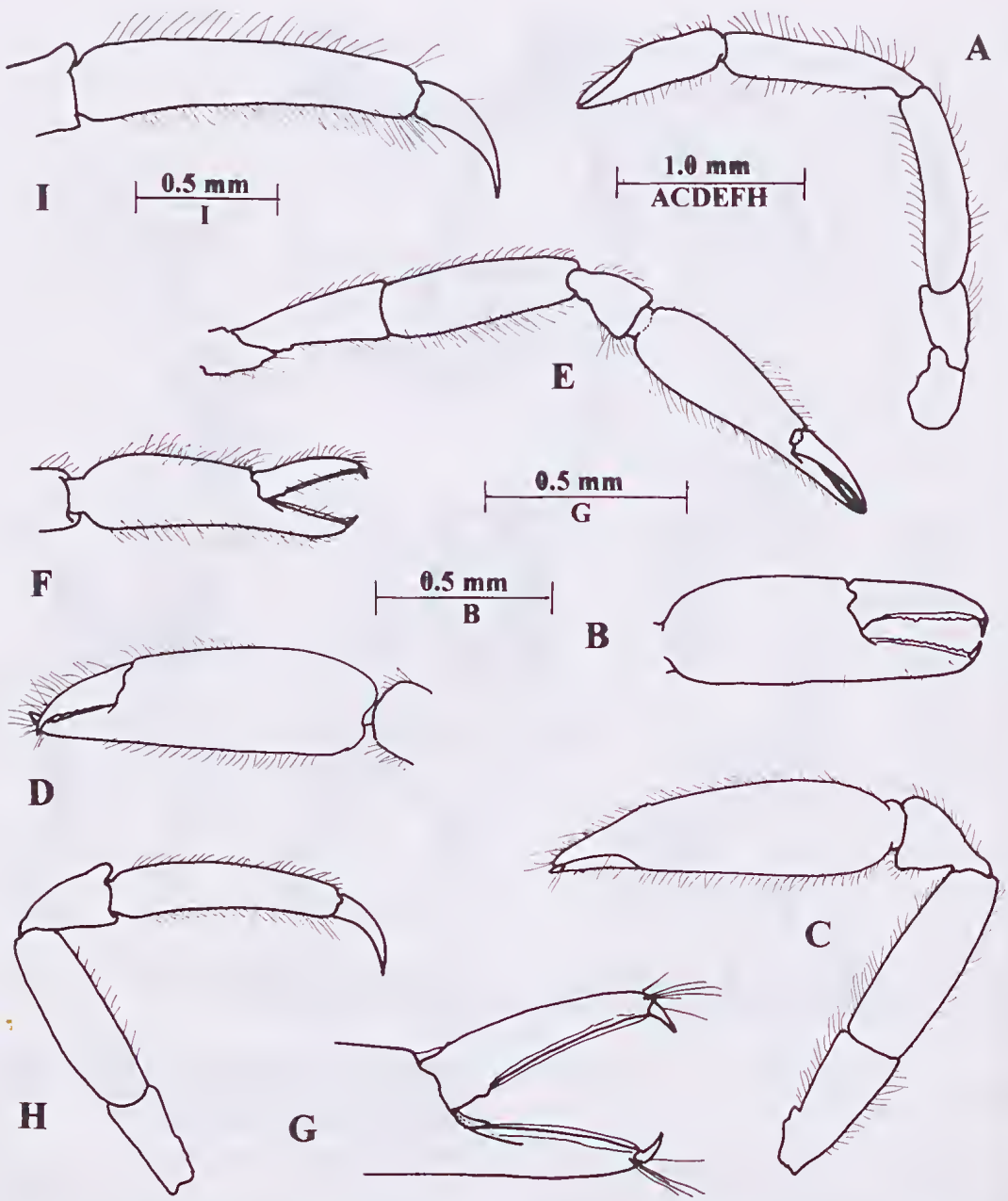


FIG. 19. *Pontonides loloata* sp. nov., paratype ♀. A, first pereiopod. B, same, chela. C, major second pereiopod, D, same, chela. E, minor second pereiopod. F, same, chela. G, same, fingers. H, third pereiopod. I, same, propod and dactyl.

HOST. *Cirripathes* sp. [Antipatharia].

COLOURATION (From colour transparency, AMPI 1455). Mainly highly transparent, carapace with two small white spots dorsally, abdomen with irregular transverse white bar across posterior of third tergite, posterior margin of sixth segment white, major second pereiopod translucent whitish.

SYSTEMATIC POSITION. *Pontonides asperulatus* sp. nov. does not appear closely related to the other species of the genus. Other species have the major second pereiopod chelae smooth and near glabrous, with the cutting edges of the fingers feebly or non-denticulate. The very well developed posterior tooth on the fifth pleuron is unique in the genus, the other species having the pleura rounded or feebly armed. The dorsal setation of the telson is also unique.

ETYMOLOGY. Latin, *asper*, rough.

REMARKS. The slender form of the single specimen suggests that it may be immature. The robust curved dactyl of the ambulatory propods is capable of an extreme degree of mobility, which suggests that it is capable of a strong grip upon the tissues of its host. The large basal plate and well developed hinge, and the deep distoventral emargination of the propod enable a wide range of flexion and extension to occur. Similar dactyls are found in all species of the genus. No information is available on the ecological situation in which these animals occur, but a specially strong grip might be required in localities subject to particularly strong currents. Similar dactyls have been noted in *Dasycaris symbiotes* Kemp 1922, and *Platycaris latirostris* Holthuis 1952 (Bruce, 1966).

**Pontonides loloata** sp. nov.
(Figs 17-21, 22F)

*Pontonides unciger*; De Grave, 2000: 142.
*Pontonides* sp. 2. Minemizu, 2000: 69.

MATERIAL. (1) 1♂, 1♀, paratypes, AMPI 1462, # 11, Milne Bay Province, 8 April 2003, QM W27226. (2) 1♀, paratype, AMPI 1464, # 16, Milne Bay, 8 April 2003, QM W27228. (3) 1 ♂ 1ovig. ♀, allotype and holotype, AMPI 1449, # 139, Loloata Island, 23 April 2003, QMW27230. (4) 1 ♂, 1 ♀, Laing Island lagoon, Hansa Bay, 5 m, 4 October 1992, coll. S. De Grave, KBIN IG 27951/NAT 274. (5) 2 juv., Davit Wreck, Hansa Bay, 9 m, 1 September 1992, coll. S. De Grave, KBIN IG 27951/NAT 274.

DIAGNOSIS. Carapace and abdomen feebly areolate, female carapace markedly gibbous, rostrum short, only to one third of length of proximal segment of antennular peduncle, distal third distinct, supraorbital carinae broadly angular angular, without distinct tooth, orbit very deep, antennal spine small, eye without dorsal tubercle, fourth and fifth pleura with acute posterodorsal tooth in male, angular in female, second pereiopods small, subequal, major chela finely tuberculate, with long setae, minor second pereiopod fingers much shorter than palm, third to fifth pereiopods with numerous long setae, sparse fusiform setae on telson.

DESCRIPTION. (1) Loloata Island specimens. – A small sized pontoniine shrimp of subcylindrical, slightly depressed body form.

Carapace (Fig. 17A) and abdomen (Fig. 17D) glabrous, dorsally smooth, pleura and branchiostegite very feebly areolate. Rostrum (Fig. 17A,B) slender, oval in section distally, unarmed, straight, reaching to near level stylocerite tips, lateral carinae obsolete on distal third, broadly expanded over bases of eyestalks, weakly angular, with obtuse lateral angle, anterior margin feebly convex, posterior border feebly concave, orbit (Fig. 17C) well developed, inferior orbital angle broadly convex, antennal spine well developed, without epigastric, hepatic or branchiostegal spines, gastric region gibbous, anterolateral angle slightly produced, rounded convex.

Abdomen (Fig. 17D) with third abdominal segment not posterodorsally produced, sixth segment about 1.6 times longer than deep, 1.5 times fifth segment length, 0.44 of CL, posterolateral angle and posteroventral angles well developed, acute, ventral surface sparsely setose, pleura of first three segments broadly rounded, fourth and fifth posteriorly produced, dorsal margin almost straight, ventral strongly convex, with acute tooth at posterodorsal angle in male (Fig. 17L,M), less marked in female (Fig. 17J,K).

Telson (Fig. 17H) length about 0.72 of CL, 1.75 times sixth abdominal segment length, 2.6 times longer than anterior width, with two pairs of small lateral marginal dorsal spines, about 0.5 mm long, at about 0.44 and 0.75 of telson length, posterior margin (Fig. 17I) about 0.3 of anterior width, rounded, without median point, with small lateral spines subequal to dorsal spines, intermediate spines robust, about 0.65 of telson length, submedian spines slender, setulose, about 0. 9 of intermediate spine length, dorsal surface of telson with sparse fusiform setae.

Antennule (Fig. 17E) with proximal segment of peduncle parallel sided, about 1.6 times longer than wide, with anterolateral angle (Fig. 20A) strongly produced, acute, reaching to slightly exceed intermediate segment of peduncle, anterolateral margin slightly produced, rounded, with single plumose seta, stylocerite short, acute, reaching to about 0.5 of segment length, without ventromedial tooth; intermediate and distal segments short and stout, combined length about 0.75 of proximal segment length; upper

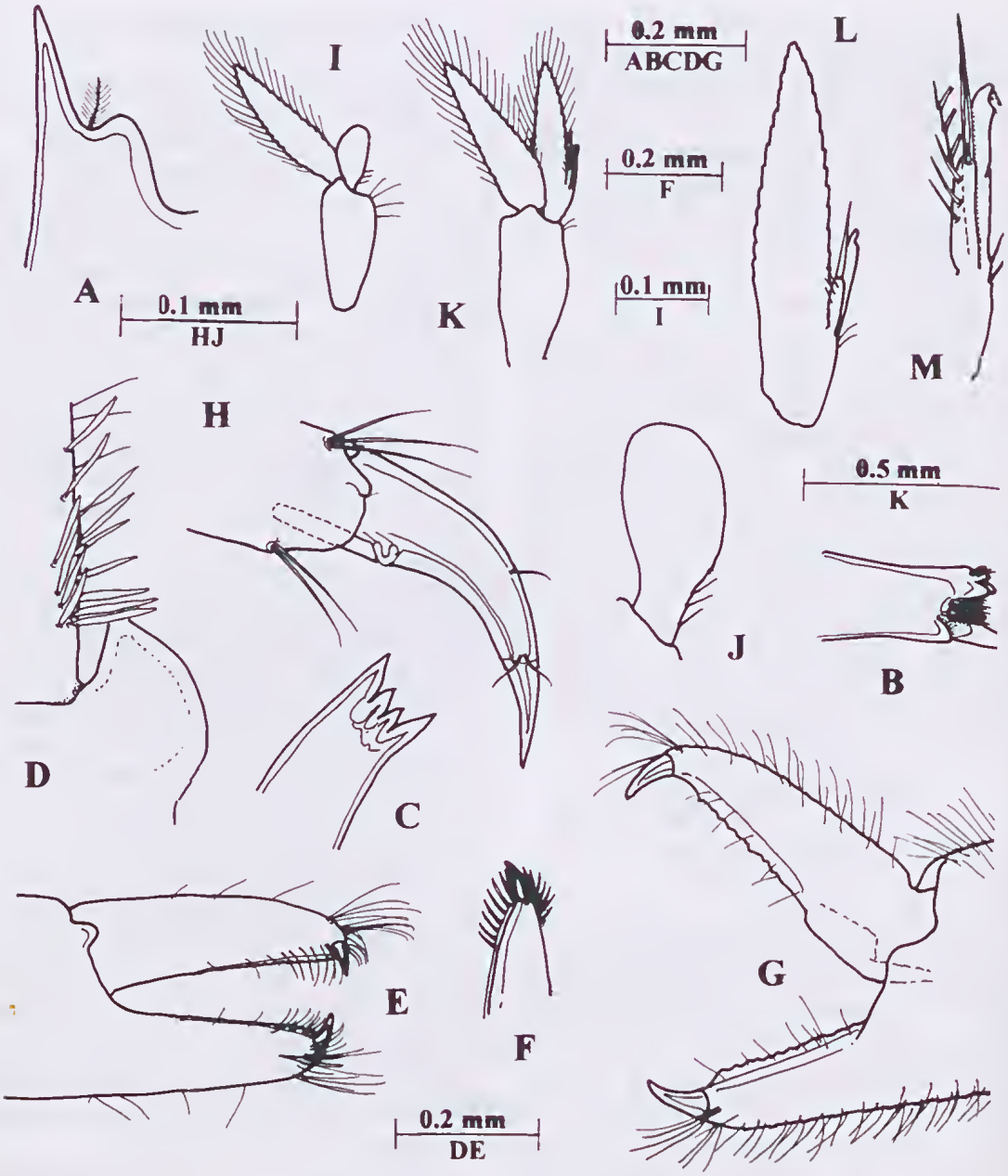


FIG. 20. *Pontonides loloata* sp. nov., paratype ♀. A, antennular pedunele, distolateral angle of proximal segment. B, mandible, molar process. C, same, incisor process. D, third maxilliped, proximal lateral margin of endopod and lateral plate of coxa. E, first pereiopod, fingers. F, same, distal daetylus. G, major second pereiopod, fingers. H, third pereiopod, distal propod and daetylus. Paratype male. I, first pleopod. J, same, endopod. K, second pereiopod. L, same, endopod. M, same, appendix masculina and appendix interna.

flagellum proximally stout, biramous, with three proximal segments fused, shorter free ramus with single segment, longer ramus filiform, with about 7 segments, with about 8 groups of aesthetascs, lower flagellum with about 11 segments.

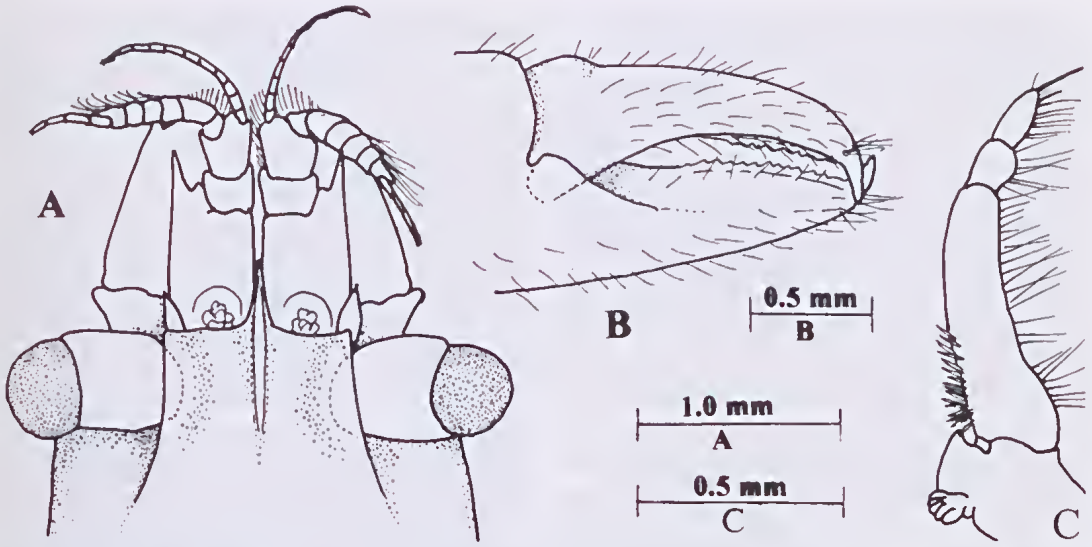


FIG. 21. *Pontonides loloata* sp. nov., ♀. Hansa Bay. A, anterior carapace and antennae, dorsal. B, third maxilliped. C, major second pereiopod, fingers.

Antenna (Fig. 17F) with stout unarmed basiccrite; carpoccrite about twiec as long as wide, flattened, reaching to about middle of intermediate segment of antennular pedunele; flagellum well developed; seaphoccrite (Fig. 17G) not exeeeding antennular pedunele, lamina broad, about 1.8 times longer than width, lateral margin slightly eonvex, with small distolateral tooth at 0.83 of lamellar length, well exeeeded by distal lamina.

Ophthalmie somite without *béc ocellaire*, with small blaek pigment spot.

Eye well developed, with hemispherieal eornea, without aecessory pigment spot, diameter subequal to stalk length, stalk without dorsal tuberele.

Mandible (Fig. 18A) without palp, molar proeess (Fig. 20B) robust, distally truneate, with five blunt teeth, with small bunch of short setae posteriorly, ineisor proeess (Fig. 20C) slender, with four distal teeth, eentral pair smaller than outer pair. Maxillula with upper laeinia (Fig. 18B) broad with six short simple spines distally and numerous longer setae, lower laeinia (Fig. 18C) with setae only. Maxilla (Fig. 18D) with well developed palp, eurved, blunt, non-setose, basal region eonvex without distinet endites, eoxal region similar, both without setae. Seaphognathite well developed, about 2.4 times longer than broad. First maxilliped (Fig. 18E) with short pointed non-setose palp, basal and eoxal endites fused, basal portion with sparse simple setae, eoxal region with few setae, exopod with large broad earidean lobe, flagellum reduced to small knob on proximal medial margin, epipod large, triangular, bilobed. Second maxilliped (Fig. 18F) with typieal endopod with daetylar segment deeply emarginate medially, with numerous robust serrulate spines, without exopod, epipod well developed with aeute posterolateral angle, without podobraneh. Third maxilliped (Fig. 18G) with robust endopod, reaehing to about proximal end of earpoeerite, proximal segment eompletely fused with basis, bowed, uniform, about 4.2 times longer than width, sparsely setose, with double rows of about 12 fusiform setae laterally on basal region (Fig. 20D), without exopod, penultimate segment about 0.2 of proximal segment length, expanded distomedially, with spines, terminal segment 2.5 times longer than wide, 1.2 times penultimate segment length, with strong terminal spine on left (lost on right?), about 0.6 of segment length, medial border spinose; lateral plate of eoxa anteriorly pointed, with small quadrilamellate arthrobraneh.

Fourth thoraeie sternite with low transverse ridge with rounded lateral teeth, fifth sternite similar, more marked, with aeute lateral teeth, sixth sternite with small longitudinal median ridge.

First pereiopod (Fig. 19A) moderately slender, all segments generally setose, exceeding the carpocerite by the carpus and chela; chela (Fig. 19B) with palm moderately compressed, about 1.75 times longer than deep, fingers (Fig. 20E) broad, about 0.75 of chela length, tapering, with well developed articulated terminal spines, surrounded by short curved setae (Fig. 20F), dactylus about 4.0 times longer than proximal depth, cutting edge lateral, weakly denticulate over distal half, with sharp entire lamella laterally, fixed finger similar, about 3.4 times longer than proximal depth; carpus about 1.25 timed longer than chela, tapering proximally, about 4.5 times longer than distal width; merus subequal to carpus length, uniform, slightly bowed, 4.7 times longer an wide; ischium 0.4 of merus length; basis typical.

Second perciopods small, unequal, dissimilar. Major second pereiopod (Fig. 19C) with chela (Fig. 19D) oval in section, 2.6 times longer than proximal depth, tapering slightly distally, 1.0 (♂) – 1.08 (♀) times CL, densely covered with minute acute tubercles particularly on lateral surface and numerous simple setae, fingers (Fig. 20G) about 0.3 of palm length, robust, with lateral cutting edges, tips stout, acute, hooked, dactylus about 3.1 times longer than proximal depth, cutting edge coarsely dentate with about 12 small irregular teeth, decreasing in size proximally, fixed finger similar, 1.8 times longer than proximal depth, cutting edge similar to dactylus; carpus short, stout, unarmed, about 0.4 of chela length, strongly tapered proximally, about 1.4 times distal width, ventral surface spinulate, setose; merus about 0.8 of palm length, 2.8 times longer than central width, subuniform, unarmed, ventral surface densely spinulate, setulose; ischium 0.7 of merus length, 2.1 times longer than distal width, tapering proximally, ventral surface spinulate, setulose; basis and coxa without special features.

Minor second pereiopod (Fig. 19E) with chela (Fig. 19F) about 0.83 of major chela length, 0.81 (♂), 0.86 (♀) of CL; palm about 2.3 times as long as proximal depth, tapering slightly distally, smooth, setose, fingers (Fig. 19G) long, slender, about 0.6 of palm length, compressed, with strongly hooked articulated tips, dactylus about 4.0 times longer than proximal depth, tapering gradually distally, with entire sharp lateral cutting edge, fixed finger similar; carpus short, stout, unarmed, setose, non-tuberculate, about 0.4 of palm length; merus subequal to palm length, unarmed, subuniform, 3.2 times longer than central width, generally densely setose; ischium 0.75 of merus length, 3.0 times longer than distal width, moderately tapering proximally, generally setose; basis and coxa without special features.

Third perciopod (Fig. 19H) robust, generally strongly setose, exceeding carpocerite by about half propodus length; dactylus (Fig. 20H) large, stout, simple, strongly curved, about 0.4 of propodus length, 4.0 times longer than proximal width, ventral edge sharply carinate, with large basal plate proximally; propodus (Fig. 19I) about 0.5 of CL bowed, 4.8 times longer than deep, tapering slightly distally, deeply emarginate distoventrally, without spines, with numerous long setae; carpus short, unarmed, about 0.45 of propodus length 1.6 times longer than distal width; merus about 0.9 of propodus length, 3.4 times longer than central width, unarmed; ischium 0.5 of meral length; basis without special features; coxa with small ventral lobe. Fourth and fifth pereiopods similar to third.

Pleopods with basipodite and rami densely setose, without special features. Male first pleopod (Fig. 20I) with endopod rounded, oval (Fig. 20J), medial margin with three simple setae proximally. Male second pleopod (Fig. 20K) with endopod (Fig. 20L) with appendices at about 0.2 of medial margin length; appendix masculina (Fig. 20M) about 0.14 of endopod length, with stout simple terminal spine about 1.4 times appendix length, with 3 shorter simple spines ventrolaterally; appendix interna about 1.5 times appendix masculina length, with few terminal cincinnuli.

Uropod with protopodite posteriorly unarmed; rami extending slightly beyond telson: exopod about 2.6 times longer than wide, lateral border setose, with small spinule at posterolateral angle, diaeresis weakly developed; endopod subequal to exopod length, 3.4 times longer than wide.

(2) Hansa Bay specimens. Generally as above, but largest specimen (Fig. 21A) much larger, with rostrum extending well beyond level of anterior margin of statocyst, to about halfway between that and the distal margin of the proximal antennular segment, with broadly rectangular lateral carinae covering the bases of the eyestalks and the proximal third of the statocyst, without lateral teeth. The third maxilliped (Fig. 21B) generally similar to the above description, with numerous fusiform setae along the lateral border of the antepenultimate segment of the endopod.

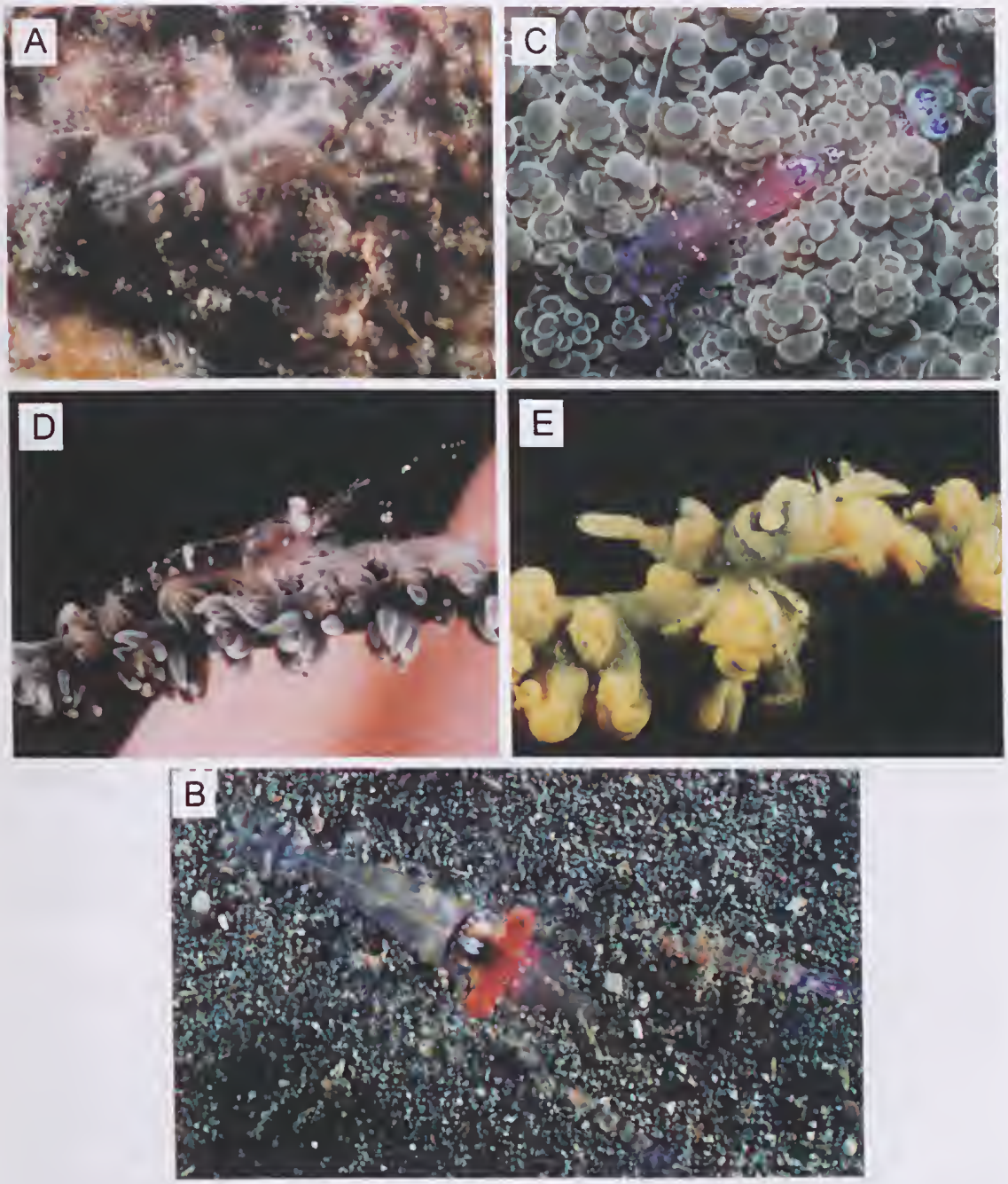


FIG. 22. A, *Colemonia litodactylus* gen. et sp. nov., holotype female. B, *Exoclimenella* sp. aff. *maldivensis* Duris & Bruce. C, *Periclimenes grandidens* sp. nov., holotype. D, *Pontonides asperulatus* sp. nov., holotype. E, *Pontonides loloata* sp. nov., holotype.

The major second pereiopod has the fingers (Fig. 21C) weakly tuberculate and gaping slightly proximally.

MEASUREMENTS (mm). Holotype ♀, carapace length, 1.8; carapace and rostrum, 2.3; total body length (approx.) 6.8; second pereiopod, major chela, 1.45; minor chela,

1.35. Allotype ♂, carapace length, 1.2; carapace and rostrum, 1.7; total body length (approx.) 4.7; second pereiopod, major chela, 1.5; minor chela, 1.3.

SYSTEMATIC POSITION. *Pontonides loloata* sp. nov. is most closely related to *P. unciger* Calman, 1939. It may be readily distinguished, particularly in large adult females, by the form of the rostrum and its lateral carinae, which are subrectangular without acute lateral teeth, with the distal rostrum non-carinate, as opposed to dentate, with the lateral carinae continuing to the rostral tip.

HOST. (1-5) *Cirripathes* sp. [Antipatharia].

COLOURATION. (From colour slide). Body and appendages, including caudal fan, generally uniform pale yellow, carapace with single broad transverse yellow band, rest of carapace and abdomen densely spotted with small light brown dots.

ETYMOLOGY. For the locality of one of the specimens, Loloata Island.

REMARKS. Both specimens (1) from Milne Bay have a distorted third abdominal tergite. This so closely resembles the condition reported in *Periclimenes hertwigi* Balss by Bruce (1972) that it seems certain that it was caused by a bopyrid isopod parasite of the genus, *Filophryxus* Bruce 1972. The type and only species of this genus is *F. dorsalis* Bruce. A photograph of the live specimens *in situ* on their host clearly shows that the parasites had already been lost prior to capture.

The colour photo provided by Minemizo (2000) shows exactly the same colour pattern as in the present specimens. In Japanese waters it occurs on *Cirripathes anguina* and *C. spiralis* at depths of 15 m and more (Minemizu, 2000). Minemizu (pers. comm., 31 October 2003) also confirms that as many as 10 specimens may occur on a single host and that the shrimps "snatch away" items of food that the host has caught. He also notes that the shrimp undergoes nocturnal colour changes, becoming translucent at night.

DISTRIBUTION. The type locality, Loloata Island, and Hansa Bay, PNG, and the Izu Peninsula, Japan.

### Pontoniopsis comanthi Borradaile, 1915

*Pontoniopsis comanthi* Borradaile, 1915: 213; 1917: 377, pl. 57, fig. 27; Holthuis, 1952: 153, figs 70-71; De Grave, 2000: 143; Li, 2000: 276, fig. 369; Davie, 2002: 337.

MATERIAL. 1 ov.♀, AMPI 1461, # 3, Milne Bay, 10 m, 7 April 2003, QM W227232.

HOST. Unidentified crinoid,.

COLOURATION (From colour transparency, AMPI 1461). Mainly very dark red-brown, with narrow pale yellow-orange dorsal stripe from rostrum to telson, more yellow posteriorly, including uropods; ambulatory pereiopods transparent, heavily banded with brown.

REMARKS. One of the smallest pontoniine shrimps, the single specimen has a CL of 1.05 mm, without special features. *Pontoniopsis comanthi* is the only Indo-West Pacific species referred to the genus and has been associated with a variety of crinoid host genera (*Comanthus, Comatula, Heterometra, Lamprometra* and *Tropiometra,* Bruce, 1982b) but more often from unidentified crinoids. The ambulatory propods in some specimens are dostoventrally unarmed (Holthuis, 1952) but others are spinose, with one, two or even three spines (Bruce, 1989). This suggests that a complex of morphologically similar species may be involved. More material from carefully identified segregated hosts will be necessary to clarify their relationships.

DISTRIBUTION. PNG – Duangit reef; Mast Wreck; Awar Wreck; Laing Island, Hansa Bay, 4-25 m, (De Grave, 2000). Other – Type locality: Mabuaig, Torres Strait, Queensland. Reported also from Israel, Kenya, Zanzibar, Seychelle Islands, Indonesia, Japan, Philippine Islands, Western Australia, Queensland, Coral Sea, Mariannas Islands, Marshall Islands, Fijian Islands and Kiribati.

### Thaumastocaris streptopus Kemp, 1922

*Thaumastocaris streptopus* Kemp, 1922: 244-247, figs 78; De Grave, 2000: 143, fig.7; Li, 2000: 286, fig. 380; Davie, 2002: 338.

MATERIAL. 1 ♂, 1 ov.♀, AMPI 1443, # 33, Loloata Island, 8 m, 11 April 2003, QM W.27231.

HOST. *Oceanapia* sp. (Phloeodictyidae, Porifera).

REMARKS. Reported in *Xestospongia testudinaria* (Lamarck) by De Grave (2000), the present specimens present no special features. Collected with specimens of *Periclimenes incertus,* see above. The association with *Oceanapia* represents a new host record.

DISTRIBUTION. PNG – Laing Island, Hansa Bay, 7-30 m, (De Grave, 2000). Other – Type locality: Nouméa, New Caledonia. Reported also from Jordan, Sudan, Somalia, Kenya, Zanzibar, Tanganyika, Madagascar, Comoro Islands, Thailand, Indonesia, Japan, Philippine Islands, Western Australia, Queensland, Caroline Islands, Marshall Islands, New Caledonia.

### Vir colemani Bruce, 2003a

*Vir colemani* Bruce, 2003a: 119, figs 1-6.

MATERIAL. (1) 1 ovig. ♀, AMPI 1351, Loloata Island, 10 m, 18 November 2001, QM W.25877.
HOST. *Plerogyra simuosa* (Dana). [Scleractinia]

REMARKS. The single specimen has the rostrum slightly exceeding the antennular peduncle, with rostral dentition of 5/1 and non-spinulate ambulatory propods. The distal dorsal rostral tooth is particularly minute. Coleman has also photographed specimens from Loloata Island in November 2001 and from Walindi, Kimbe Bay, New Britain in December 1999 with the same colour pattern.

DISTRIBUTION. PNG– Type locality: Loloata Island, Port Moresby, 10 m, on *Plerogyra paradivisa* Veron, 1990. Other – Nil.

### Vir philippinensis Bruce & Svoboda, 1984

*Vir philippinensis* Bruce & Svoboda, 1984: 87, figs 1-4; De Grave, 2000: 145; Li, 2000: 302, fig. 405; Davie, 2002: 340.

MATERIAL. 1♀ , AMPI 1349, Loloata Island, 25 m, 19/20 April 2001, QM W.25876.
HOST. *Plerogyra simuosa* (Dana) [Scleractinia].

REMARKS. The single specimen has a rostral dentition of 8/2 and spinulate ambulatory propods.

DISTRIBUTION. PNG – Loloata Island (Coleman, 1998); Laing Island; Mast Wreck, Hansa Bay, 7-10 m; on *Euphyllia glabrescens* (De Grave, 2000). Other – Type locality: Cebu, Philippine Islands, 20-30 m. Red Sea, Myanmar, Indonesia, Japan, Western Australia, and Queensland.

## DISCUSSION

### (1) FURTHER REMARKS ON THE INDO-WEST PACIFIC "*PONTONIA*-LIKE" PONTONIINE GENERA

*Pontonia* Latreille, 1829, *sensu lato* has been revised by Fransen (2002) and divided into six genera. *Colemonia* gen. nov. increases the number of genera to seven. His detailed review indicates that *Dactylonia* Fransen, then had six species [to which has been added *D. franseni* Bruce, 2003b], includes *D. medipacifica* (Edmondson, 1935) which exhibits many features that contrast markedly with the other species. A new genus is now proposed for Edmondson's species.

### Cainonia gen. nov.

DIAGNOSIS. Small, robust, subcylindrical, slightly depressed body. Rostrum very short, acute, unarmed, with preterminal setae ventrally, dorsal carina feebly developed, lateral carinae broad, not covering bases of eyestalks; carapace glabrous, inferior orbital angle obsolete, antennal spine acute, orbit feebly obsolete, supraorbital, epigastric and hepatic spines absent, anterolateral angle rounded, not produced. Abdomen with posterior segments depressed, pleura rounded, sixth segment with posterolateral angle reduced, posteroventral angle small, blunt. Telson with two pairs of large sub-marginal dorsal spines, three pairs of posterior spines. Eye normal, with hemispherical cornea. Antennule with ventromedial tooth on basal segment minute or absent, anterolateral tooth small, not exceeding half length of intermediate segment, flagella reduced. Antenna with basicerite unarmed, scaphocerite well developed, with distolateral tooth not exceeding lamella, less than 0.1 of lamellar length. Third thoracic sternite without large triangular transverse median plate, fourth unarmed, fifth and sixth with pairs of low acute lateral plates, sixth, seventh and eighth unarmed. Mandible with slender corpus, without palp, molar process subcylindrical, incisor process with oblique set of four acute teeth distally, without denticles along medial border. Maxillula with feebly bilobed palp, upper lacinia normal. Maxilla with reduced simple basal endite with single distal seta, scaphognathite broad. First maxilliped with slender palp, basal endite large, broad, laterally convex, medially sublinear, with numerous long finely serrulate setae, distinct from densely setose coxal endite, exopod well developed with narrow caridean lobe, flagellum with 4-5 plumose terminal setae, epipod large, feebly bilobed. Second maxilliped endopod with dactylar segment normal, basis without medial angulation, exopod flagellum well developed with 4 plumose terminal setae, epipod small, rounded, without podobranch. Third maxilliped with ischiomerus partly fused to basis, endopod slender, antepenultimate segment slightly broader than distal segments, exopod flagellum well developed with numerous plumose terminal setae, coxa without medial process, with large rounded lateral plate, without arthrobranch. First pereiopods robust, with simple chelae. Second pereiopods with robust chelae, similar, subequal, palm glabrous, smooth, without ventral carina, fingers without molar process and fossa, dactylus with single small tooth, fixed finger with two

TABLE 2. Comparison of *Dactylonia* and *Cainonia*. w/wo=with or without

| Character | *Dactylonia* | *Cainonia* |
|---|---|---|
| Rostrum | Well developed, acute | Greatly reduced, acute, short, not covering bases of eyes |
| Lateral carinae | Narrow | Broad |
| Postrostral region | Carinate | Feebly carinate |
| Inferior orbital angle | Feebly developed | Obsolete |
| Antennal spine | Acute | Acute, small, broad |
| Pterygostomial region | Rounded, not produced | Rounded, slightly produced |
| Ventromedial tooth on proximal antennular segment | Small | Minute or absent |
| Distolateral tooth | Reaching beyond middle of intermediate segment | Small, not reaching beyond middle of intermediate segment |
| Anterolateral tooth of scaphocerite | <0.1 of scaphocerite length, usually exceeding lamella | 0.1 of scaphocerite length, not exceeding lamella |
| Maxilla, basal endite | Small, bilobed, proximal lobe sometimes obsolescent, sparsely setose | Short, simple, obsolescent, with single seta |
| Coxal endite | Distinct | Obsolete |
| Basal endite of first maxilliped | Broad, densely setose, forming basket | Broad, numerous long setae, not forming basket |
| Epipod of first maxilliped | Oval | Large, elongate, feebly bilobed |
| Epipod of second maxilliped | Rounded | Trapezoidal, proximally expanded |
| Third maxilliped endopod, articulation of ischiomerus and basis | Partly fused | Partly fused, suture indistinct |
| Combined segment form | Broad or narrow, not semi-operculate | Narrow, not semi-operculate |
| Distal segments | Elongate, little longer than combined segment | Elongate |
| Terminal segment | Densely setose | Numerous long setae |
| Fourth thoracic sternite | w/wo triangular medially notched plate | Transverse lateral plates |
| Second pereiopod chelae | Unequal, dissimilar | Subequal, similar |
| Cross section | Ventrally carinate, usually serrate | Oval, non-carinate |
| Third pereiopod dactyl | | |
| Setation of corpus | Well-developed | Numerous slender setae |
| Accessory tooth | Acute, unarmed or feebly denticulate | Blunt, densely microdenticulate |
| Ventral dentition | Elongate, acute or blunt, sometimes distally swollen with microdenticulations | Short blunt club-like teeth |
| Unguial microspinulation | Sparse denticulations distally | Densely microspinulate |
| Propod, distoventral spines | Well-developed, acute | Present, blunt |
| Ventral spines | Present | Absent |
| Sixth abdominal segment, posterolateral tooth | Acute, generally well-developed | Blunt, obsolete |
| Posteroventral tooth | Large, broad, acute | Reduced, blunt |
| Telson, dorsal spines | Very large, submarginal, usually grouped on anterior half | Large, submarginal, on anterior half |
| HOST | Ascidian | Bivalve mollusc |

small acute teeth distally, both sparsely setose, proximal segments unarmed. Ambulatory pereiopods slender, dactylus biunguiculate, with unguis distinct, densely covered with microdenticulations, corpus with distoventral tooth similar to but smaller than unguis, ventral margin with 12-13 blunt club-like teeth, of decreasing size proximally, devoid of distal microdenticulations, corpus with numerous dorsal and ventral setae, propod with pair of slender distoventral spines only. Uropod with protopodite unarmed, exopod with distolateral spinule only.

TYPE SPECIES. *Pontonia medipacifica* Edmondson, 1935. The genus is monospecific.

ETYMOLOGY. Greek *kainos*, new, and *Pontonia*, a name first used by Latreille (1829). Gender feminine.

HOSTS. Associated with spondylid bivalve molluscs.

SYSTEMATIC POSITION. *Cainonia* is most closely related to *Dactylonia* Fransen (2002). The similarities and differences are detailed in Table 2.

The major features that distinguish *Cainonia* gen. nov. from *Dactylonia* Fransen 2002 are the very short rostrum that does not cover the bases of the eyestalks, the obsolete orbit and inferior orbital angle (see below), the strongly reduced basal endite and obsolete coxal endite of the maxilla, the subequal, similar, non-carinate second pereiopod chelae, and the blunt densely microspinulate unguis and accessory tooth of the ambulatory pereiopods, with the short blunt club-like ventral tubercles on the corpus, and blunt distoventral spines on the ambulatory propod. The host association, unlike all other *Dactylonia* species is with a spondylid bivalve mollusc.

The "antennal spine" in this species may actually be the expanded inferior orbital angle, in which case the antennal spine would be absent. The generic definition would then be revised to "inferior orbital angle acute, antennal spine absent" in place of "inferior orbital angle obsolete, antennal spine acute".

The only other "*Pontonia*-like" genus associated with bivalve hosts is *Bruceonia* Fransen, 2002, which was found in *Chama pacifica* Broderip, 1835. The single species, *B. ardeae* Bruce, is readily distinguished from *C. medipacifica* by the presence of a well developed stout rostrum and a generally hirsute body and appendages. It is known only from its type locality on the Great Barrier Reef.

### Cainonia medipacifica (Edmondson, 1935) comb. nov.

*Pontonia medipacifica* Edmondson, 1935: 6, fig.2; Bruce, 1980b: 225, figs 1-4; Li, 2000: 265, fig. 351.
*Dactylonia medipacifica*; Fransen, 2002: 307, figs 202-208.

HOLOTYPE. Ovigerous ♀, BM S.3845 from Midway Island, Hawaiian Islands.

HOST. *Spondylus varians* Sowerby 1847 [Mollusca: Spondylidae].

DISTRIBUTION. Ambon, Indonesia; Ifaluk Atoll, Caroline Islands, and the Hawaiian Islands.

## A REVISED KEY TO THE GENERA OF "*PONTONIA*" SENSU LATU (based on Fransen, 2002)

1. Rostrum stout, thickened, without distinct dorsal, ventral or lateral carinae, suboval in section; body and appendages generally sestose: ambulatory dactyls simply biunguiculate.....*Bruceonia* Fransen

Rostrum with distinct carinae, T or + shaped in section .....2

2. Rostrum greatly reduced, not covering bases of eyestalks, with ventral carina, maxilla with strongly reduced basal endite and obsolete coxal endite; subequal, similar, non-carinate second pereiopod chelae; blunt densely microspinulate unguis and accessory tooth on dactyls of ambulatory pereiopods, with short blunt club-like ventral tubercles on the corpus, blunt distoventral spines only on ambulatory propod. . . . . *Cainonia* gen. nov.

Rostrum well developed, covering bases of eyestalks . 3

3. Rostrum with 2-3 distinct dorsal teeth, lateral carinae not developed. . . . . *Rostronia* Fransen

Rostrum without or with one small subdistal dorsal tooth, with developed lateral carinae. . . . . 4

4. Ventromedial tooth on proximal antennular segment large5

Ventromedial tooth on proximal antennular segment small. . . . . 6

5. Ambulatory dactyls generally biunguiculate, setose, with accessory ventral teeth; propod with feebly developed distoventral spines; third maxillipeds not sub-operculiform, third thoracic sternite without transverse median plate . . . . . *Odontonia* Fransen

Ambulatory dactyls simple, glabrous; propod with well developed distoventral spines; third maxillipeds sub-operculiform, third thoracic sternite with large triangular transverse median plate *Colemonia* gen. nov.

6. Dactyls of ambulatory pereiopods with flexor margin dentate or tuberculate; rostrum with dorsal carina; first maxilliped endites forming basket . . . . . *Dactylonia* Fransen

Dactyls of ambulatory pereiopods with flexor margin unarmed; rostrum without dorsal carina; first maxilliped endites not forming basket. . . . . 7

7. Rostrum with subdistal ventral tooth; antennal spine distinctly separated from infraorbital margin, acute; scaphocerite with distolateral tooth less than 0.1 of length of scaphocerite; submedian carinae of corpus of paragnath parallel, setose; alae of paragnath medially rounded; proximal pair of dorsal spines at 1/3 to ½ of telson length; distal pair of dorsal spines on distal third of telson . . . . . ...*Pontonia* Latreille

8. Rostrum without ventral teeth; antennal spine merged with inferior orbital angle, blunt (acute in *Ascidonia flavomaculata*); scaphocerite with distolateral tooth more than 0.2 of length of scaphocerite; submedian carinae on corpus of paragnath oblique, non-setose, alae of paragnath medially bilobed or excavate; proximal pair of dorsal spines at ¼ of telson length; distal pair of dorsal telson spines on proximal half of telson . . . . . *Ascidonia* Fransen

*Dactylonia* sp. from New Caledonia (Bruce, 2003: 305) was not correctly identified originally (Bruce, 1996) and was later referred to an un-named species. To clarify the placement of this taxon it is here provided with a name.

### Dactylonia borradalei sp. nov.

Not *Pontonia ascidicola* Borradaile, 1898: 389; 1899: 409, pl. 36, fig. 6.
*Pontonia ascidicola*; Bruce, 1996: 241, fig. 29 g, h.
*Dactylonia ascidicola*; Fransen, 2003: 284 (*partim*).

*Dactylonia* sp. Bruce, 2003b: 305.

DIAGNOSIS. Generally closely similar to *Dactylonia ascidicola* Borradaile, 1898. Differs from that species, and all others of the genus, in the presence of a minute comb with fine pectinations on the ventral proximal margin of the unguis of the third ambulatory pereiopod (Bruce, 1996, fig. 29g), and a propod without distal or ventral spines (Bruce, 1996, fig. 29g). The ventral accessory dentieles of the ambulatory corpus also are distally swollen (Bruce, 1996, fig. 6h) and without mierodenticulations, rather than distally truncate and mierodenticulate as in *P. ascidicola* (Fransen, 2002, fig. 191b,c). The unguis is also without distodorsal scales, which are present in *D. ascidicola.*

TYPES. Ovigerous ♀ holotype, ♂ allotype, MNHN-Na 12889, from Neokumbi Reef, New Caledonia, 20-40 m.

ETYMOLOGY. In honour of Lancelot Alexander Borradaile (1872-1945), formerly Lecturer in Zoology in the University of Cambridge, Fellow, Dean and Lecturer of Selwyn College, who published in 1917 the first major monograph *On the Pontoniinae,* in recognition of his major contribution to pontoniine shrimp studies.

HOST. *Ascidea sydneiensis* Stimpson, 1854.[Ascidiacea]

DISTRIBUTION. Known only at type locality.

REMARKS. The absence of spines from the ambulatory propod is a feature that requires a slight modification for the generic diagnosis for its inclusion.

*Dactylonia franseni* was described on the basis of a single example from Mombasa, Kenya (Bruce, 2003b). It was considered that the unusual rostrum was probably abnormal. A further example from the same locality has now become available, which enables the normal rostrum to be described.

### Dactylonia franseni Bruce, 2003b

*Pontonia* sp. Bruce, 1976b: 483.
*Dactylonia franseni* Bruce, 2003b: 299, figs 1-4.

MATERIAL. 1♂, Nyali, Mombasa Old Port, Kenya, AJB #2107, 6 m, 15 February 1974, coll. J. Wood, scuba, from bridge mooring chains, RMNH D 50658.

REMARKS. The rostrum is narrow, about three times longer than the basal width, scarcely covering the bases of the eyestalks, reaching to about 0.5 of the length of the basal antennular segment, very acute in lateral view, dorsal carina strongly convex, ventral margin straight, without distal setae.

HOST. Not recorded, presumably as for holotype, *Ascidia sydneiensis.* Colouration noted as transparent, with scattered large yellow chromatophores all over body and appendages.

MEASUREMENTS (mm). Carapace length, 2.3; carapace and rostrum, 3.3; second pereiopod, major chela, 5.0; minor chela, 4.0.

DISTRIBUTION. Known only from the type locality, Nyali, Mombasa, Kenya.

## (2) FURTHER REMARKS ON SPECIES OF *PONTONIDES* CALMAN

The few species of *Pontonides* Calman, 1939 are not well known. In addition to the species reported on above, only two other species have so far been described in the literature from the Indo-West Pacific region, *Pontonides maldivensis* (Borradaile, 1915), and *P. unciger* Calman, 1939.

*Pontonides maldivensi* may be readily distinguished from all other known species by the form of the lateral rostral carinae. In Borradaile's illustration (Borradaile, 1917, pl. 57, fig. 28b) this appears strongly and smoothly concave. Actually, in the type material, it is weakly bi-concave, with a slight angulation between the two curved edges, and is without any trace of a tooth. This indicates a closer resemblance to the other species of the genus than was apparent.

*Pontonides unciger*, as described by Calman (1939), is a species with an acute tooth on the lateral rostral carinae, a smooth carapace and abdomen; the eyestalk without a dorsal tubercle, the second maxilliped with a number of fusiform setae along the proximal dorsal margin of the endopod; similar setae present on the third maxilliped but without such setae on the second pereiopods. These features all contrast with the *Siboga* specimen described as *P. unciger* by Holthuis (1952), which is now reported as a new species.

The holotype of *P. unciger,* BMNH 1939.10.9.306, has been re-examined. It is mainly intact, but now lacking both second pereiopods. Dissected antennae, mouthparts and first pereiopod on the right side are missing. It can be confirmed that the carapace and abdomen are smooth and the eye lacks a dorsal tubercle. It may be noted that the third sternite is with a broad based, laterally concave, distally acute transverse plate and the pleuron 4 and 5 both bear a small but distinct acute posterior tooth. The

pereiopods and telson are sparsely setose. About 20 ova are present.

Many records of *P. uneiger* should be re-assessed. Some of these probably do not belong to *P. uneiger* s.str. *Pontonides uneiger* has been reported from: Madagascar: Nosy Tanga (?) (Bruce, 1978b); Seychelle Islands: Desroches Atoll,15 m; Bird Island, 20 m; Poivre Atoll, 15 m (Fransen,1994); Maldive Islands: North Nilandu Atoll, Genego Island, 50 m (*Pontonides ? unciger* Duris, 1990); Queensland: Broadhurst Reef, 5 m (Zann, 1980); Wistari Reef (?) (Bruce, 1983); Taiwan: Kentin National Park, Ping-Tong (Jeng, 1998); Japan: Amakusa Island (Kikuchi & Miyake, 1978); Hawai'i: no locality (Gosliner, et al., 1996). There are also many photographs of the same or a very similar shrimp in non-scientific publications, often on antipatharian hosts such as *Cirripathes anguinis*. The species with two broad transverse yellow bands across the carapace, often referred to *P. unciger*, such as in Debelius (2001: 194) is a distinct innominate species.

The identification of the specimens, from Mombasa, Kenya (Bruce, 1976b), can be confirmed. The specimens were found in association with unidentified bushy antipatharian hosts, from 26-30 metres. The *Pontonides* specimens from Takuata, Marquesas Islands have been excellently described and illustrated in considerable detail by Monod (1979), who confirms the presence of fusiform setae (which he suggests may be aesthetases) on the second and third maxillipeds, so that these specimens also may be safely attributed to *P. uneiger* Calman. However, he does not mention or illustrate a tooth on the fifth pleuron. The single host is not identified but as about 30 specimens were obtained, it is likely to have been a bushy specimen and not a *Cirripathes*.

*Pontonides* is represented in the eastern Pacific region by *P. sympathes* De Ridder & Holthuis, 1979, from the Galapagos Islands. This species resembles the species named below in having a distinct dorsal tubercle on the eyestalk but differs in having a very short rostrum with dentate lateral carinae.

### Pontonides sibogae sp. nov.

*Pontonides unciger*; Holthuis, 1952: 249, figs 108-112; Fujino & Miyake, 1969: 87, fig. 1.

DIAGNOSIS. Lateral rostral carinae angular, without conspicuous acute lateral tooth, branchiostegite and pleura with areolate depressions, posterior pleura without posteroventral teeth, eyestalk with dorsal tubercle, second and third maxillipeds without fusiform setae, fusiform setae present along dorsal margin of ischium of second pereiopods.

HOLOTYPE. ♀, ZMA De204639 from Siboga Station 49a, Sape Strait, Indonesia, 23° 30'S, 119° 4.6'E, 70 m, 14 April 1899, ZMA De 204639.

ETYMOLOGY. After the Netherlands research vessel *Siboga*, which supported the 1899-1900 expedition to Indonesia during which this species was collected..

SYSTEMATIC POSITION. Most closely related to *Pontonides uneiger*, this species is readily distinguished by the characters provided in the diagnosis above.

HOST. Not recorded.

DISTRIBUTION. Known with certainty only from the type locality and Japan.

REMARKS. The specimens described by Fujino & Miyake (1969) are reported to agree exactly with the description of Holthuis (1952) and are therefore considered to belong to *P. sibogae* rather than *P. uneiger* Calman. The second pereiopods are particularly variable, but most of those illustrated show the presence of the characteristic fusiform setae on the ischium. They were found in association with the scleractinian coral *Dendrophyllia ijimai* Yabe, collected from 54-72 m, at a similar depth to the holotype.

### A KEY TO THE INDO-WEST PACIFIC SPECIES OF *PONTONIDES* BORRADAILE, 1917

1. Body surface distinctly areolated; supraorbital carina dentate; eye with dorsal tubercle, second pereiopod ischium with fusiform setae. . . . . *P. sibogae* sp. nov.
   Body surface not strongly areolate; eye without dorsal tubercle, second pereiopod ischium without fusiform setae . . . . . 2
2. Supraorbital carina generally convex, without distinct tooth, extending almost to rostral tip, with lateral tooth obsolete; third maxilliped without fusiform setae, second pereiopod ischium with fusiform setae; minor chela with fingers 1.5 times longer than palm; fourth and fifth pleura rounded . . . . *P. maldivensis* (Borradaile)
   Lateral margins of supraorbital carinae angular or convex . . . . . 3
3. Supraorbital carina subrectangular, without acute tooth, rostrum not exceeding level of tip of stylocerite; third maxilliped only with ischial fusiform setae; second pereiopods small, subequal; fifth pleuron with small tooth at most . . . . . *P. loloata* sp. nov.
   Supraorbital carina with acute tooth . . . . . 4

4. Rostrum reaching to distal margin of proximal segment of antennular peduncle, distally distinct from lateral carinae; second pereiopods markedly unequal, densely covered with short erect setae, minutely denticulate; minor second pereiopod with fingers subequal to palm length; fifth pleuron with very large posterodorsal tooth, fourth pleuron rounded . . . . . *P. asperulatus* sp. nov.

Rostrum not reaching to distal margin of proximal segment of antennular peduncle, lateral carinae extending to rostral tip; major second pereiopod chela sparsely covered with long setae, minor chela with fingers about half palm length, minutely denticulate; fourth and fifth pleura weakly armed *P. unciger* Calman

## (3) AN ANNOTATED CHECKLIST OF THE PAPUA NEW GUINEAN PONTONIINE SHRIMP FAUNA

The pontoniine fauna of Melanesia as a whole has been summarized by De Grave (2001). The more restricted fauna of PNG is summarized below. The pontoniine shrimp fauna is raised to 64 taxa, with four species of uncertain speeifie status, belonging to 32 gencra. *Periclimenes* is the largest genus, with 35 species, more than half the total number. Most are well known Indo-West Pacific coral reef speeies and probably represent only a small fraction of the total pontoniine fauna present.

*Anchiopontonia hurii* (Holthuis, 1981)
Hansa Bay, 9-19 m, in *Spondylus varius* (De Grave, 1999)

*Anchistus australis* Bruce, 1977
Hansa Bay, 5-15 m, in *Tridacna gigas, T. squamasus* (De Grave, 1999)

*Anchistus custoides* Bruce, 1977
Hansa Bay, 6-15 m, in *Pinna bicolor, Atrina vexillum* (De Grave, 1999)

*Anchistus custos* (Forsskål, 1775)
Hansa Bay, 19 m, in *Pinna bicolar* (De Grave, 1999)

*Anchistus demani* Kemp, 1922
Hansa Bay, 3-6 m, in *Tridacna squamosa, T. maxima* (De Grave, 1999)

*Anchistus miersi* (De Man, 1888)
Dobu, D'Entrecasteaux Islands (Borradaile, 1898). Hansa Bay, 3-19 m, in *Magnavicula penguin, Tridacna maxima* (De Grave,1999)

*Apopontonia dubia* Bruce, 1981
Davit Wreck, Hansa Bay, 10 m (De Grave, 2000)

*Apopontonia falcirostris* Bruce, 1976
Laing Island lagoon, Hansa Bay, 5-25 m, in *Xestospongia testudinaria* (De Grave, 2000)

*Colemonia litodactylus* gen. et sp. nov. Above.

*Conchodytes biunguiculatus* Paulson, 1875
Hansa Bay, 7m, in *Streptopinna saccata* (De Grave, 1999)., Duangit, Hansa Bay, and Potsdam Islands and Purar Island reef, 10-45 m (De Grave, 2000)

*Conchodytes meleagrinae* Peters, 1852. Above.

*Conchodytes monodactylus* Holthuis, 1952
Hansa Bay, 20 m, in *Maguavicula pinguin* (De Grave, 1999)

*Coralliocaris superba* (Dana, 1852)
Mast Wreek, Hansa Bay, 3 m (De Grave, 2000)

*Coralliocaris viridis* Bruce, 1974
Madang (Morgan, 1988).

*Dactylonia ascidicola* (Borradaile, 1898)
Laing Island, Hansa Bay (De Grave, 2000).

*Dasycaris zanzibarica* Bruce, 1973. Above.

*Exoclimenella sibogae* (Holthuis, 1952)
Davit Wreck, Hansa Bay, 10 m, (De Grave, 2000); Hansa Bay, Laing Island, 15 m, in *Seriatopora hystrix* (De Grave, 2000).

*Exoclimenella maldivensis* Duris & Bruce, 1995
Laing Island, Hansa Bay; Wanginam Bay, 15 m, in *Seriatopara hystrix* (De Grave, 2000)

*Exoclimenella* aff. *maldivensis*. See above.

*Fennera chacei* Holthuis, 1951
Awar Wreck; Laing Island; Davit Wreck, Hansa Bay, 6-10 m, in *Pocillopora damicornis* (De Grave, 2000).

*Hamodactylus boschmai* Holthuis, 1952
Loloata Island (Coleman, 1998).

*Hamodactylus noumeae* Bruce, 1970
Laing Island, Hansa Bay, 5 m, in *Pocillopora damicornis*, (De Grave, 2000).

*Hamopontonia corallicola* Bruce, 1970
Loloata Island (Coleman, 1998). Laing Island, Hansa Bay, to 6 m, on *Heliafungia actiniformis*, (De Grave, 1998).

*Harpiliopsis beanpresii* (Audouin, 1825)
Laing Island, Hansa Bay, 5 m, in *Pocillapora damicornis*, (De Grave, 2000).

*Harpiliopsis depresssa* (Stimpson, 1860)
Madang (Morgan, 1988). Laing Island, Hansa Bay, 5-15 m, in *Pocillopora damicornis, Seriatopora hystrix*, (De Grave, 2000).

*Harpiliopsis spinigera* (Ortmann)
Laing Island; Mast Wreck, Hansa Bay; Potsdam Island, 3-10 m, in *Pocillopora damicornis, Stylophora pistillata* (De Grave, 2000).

*Harpilius lutescens* Dana, 1852
Laing Island, Hansa Bay, in *Pocillopora damicornis* (!!) (De Grave, 2000).

*Ischnopontonia lophos* (Barnard, 1962)
Laing Island, Hansa Bay, 7-20 m, in *Galaxea fascicularis, Acrhelia horresceus* (De Grave, 2000).

*Jocaste japonica* (Ortmann, 1890)
Laing Island; Mast Wreck, Hansa Bay, 3-15 m, in *Acropora* sp., (De Grave, 2000).

*Jocaste lucina* (Nobili, 1906)
Laing Island, Hansa Bay, 5-10 m, in *Pocillopora damicornis, Acropora* sp., (De Grave, 2000).

*Kemponia* aff. *agag*. Above.

*Kemponia amymone* (De Man, 1902)
Sisimangum, Hansa Bay, 5-6 m (De Grave, 1999). Laing Island; Awar Wreck Hansa Bay,; 3-15 m; in *Acropora* sp., *Seriatopora hystix, Pocillopora damicornis* (De Grave, 2000).

*Kemponia elegans* (Paulson, 1875)
Laing Island, Hansa Bay, intertidal (De Grave, 2000).

*Kemponia ensifrons* (Dana, 1852)
Laing Island; Duangit reef; Awar village; Hansa Bay, intertidal to 35 m (De Grave, 2000).

*Kemponia grandis* (Stimpson, 1860)
Laing Island; Duangit reef, Hansa Bay; Purar Island reef; intertidal to 15 m; (De Grave, 2000). .

*Kemponia kororensis* (Bruce, 1977)
Laing Island, Hansa Bay, to 10m, on *Heliofungia actiniformis* (De Grave, 1998).

*Kemponia laeertae* (Bruce, 1992)
Laing Island, Hansa Bay, 15 m (De Grave, 2000).

*Kemponia longirostris* (Borradaile, 1915)
Beagle Bay (as *Palaemonella rotumana*), (Nobili, 1899).

*Kemponia platycheles* (Holthuis, 1952)
Laing Island, Hansa Bay, 15m; in *Seriotopora hystrix* (De Grave, 2000).

*Kemponia seychellensis* (Borradaile, 1917)
Beagle Bay (as *Periclimenes tenuipes*), (Nobili, 1899).

*Kemponia tennipes* (Borradaile, 1898)
Ralun, New Britain (Borradaile, 1900). Loloata Island (Coleman, 1998). Laing Island, Hansa Bay, 10-30 m (De Grave, 2000).

*Manipontonia psamathe* (DeMan, 1902). Above.

*Odontonia sibogae* (Bruce, 1972)
Laing Island, Hansa Bay, (De Grave, 2000).

*Onycoearidella monodoa* (Fujino & Miyake, 1969)
Laing Island, Hansa Bay, 10 m, (De Grave, 2000).

*Orthopontonia ornata* (Bruce, 1970)
Davit Wreck; Sushi Maru Wreck; Mast Wreck, Hansa Bay, (De Grave, 2000).

*Palaemonella pottsi* Borradaile, 1915
Hansa Bay, Laing Island; Duangit reef; 1-30 m (De Grave, 2000).

*Palaemonella pusilla* Bruce, 1975
Madang (Bruce, 2002).

*Palaemonella rotumana* (Borradaile, 1898)
Beagle Bay (Nobili, 1899, as *Periclimenes vitiensis*). Laing Island; Davit Wreck; Duangit reef; Purar Island reef, Hansa Bay; Potsdam Island; 3-45 m (De Grave, 2000).

*Paranchistus armatus* (H.- M. Edwards, 1837)
New Ireland (H. Milne Edwards, 1837). Hansa Bay, in *Tridacna gigas* (De Grave, 1999).

*Paranchistus pyenodontae* Bruce, 1978
Hansa Bay, 9-10 m, in *Hyotissa hyotis*, *Magnavicula penguin* (De Grave, 1999).

*Periclimenaeus bidentatus* Bruce, 1970
Mast Wreck; Hansa Bay, 8m, in sponges (De Grave, 2000).

*Periclimenaeus nobilii* Bruce, 1974
Laing Island, Hansa Bay, (De Grave, 2000).

*Periclimenella spinifera* (De Man, 1902)
Beagle Bay, (as *Periclimenes tridentata*), (Nobili, 1899). Laing Island; Hansa Bay, 3-10 m (De Grave, 2000).

*Periclimenes affinis* (Zehntner, 1895)
Wanginam reef; Duangit reef'; Laing Island; Hansa Bay, 6-30 m (De Grave, 2000).

*Periclimenes amboinensis* (DeMan, 1888). Above.

*Periclimenes attenuatus* Bruce, 1971
Laing Island, Duangit Reef, Hansa Bay, 1-15 m, on crinoids (De Grave, 2000).

*Periclimenes brevicarpalis* (Schenkel, 1902)
Madang (Morgan, 1988). Loloata Island (Coleman, 1998), Milne Bay (Coleman, 2000). Laing Island; Hansa Bay, 1-5m; on *Macrodactyla doreensis* (De Grave, 2000).

*Perielimenes ceratophthalmus* Borradaile, 1915. Above.

*Periclimenes commensalis* Borradaile, 1915
Duangit reef; Wanginam reef; Hansa Bay, 3-20 m; on crinoids (De Grave, 2000).

*Periclimenes grandidens* sp. nov. Above.

*Perielimenes holthuisi* Bruce, 1969
Kranket Island, Madang (Bruce, 1977). Loloata Island (Coleman, 1998). Duangit reef, Hansa Bay, 20 m (De Grave, 2000).

*Periclimenes* aff. *holthuisi* Bruce, 1969. Above.

*Periclimenes imperator* Bruce, 1967
Loloata Island (Coleman, 1998). Milne Bay, on *Risbecia tryoni*; Tufi (Debelius, 1999). Awar; Laing Island; Bisal Paap reef, Hansa Bay, 5-30 m; on *Stichopus vorlegotus*, *Enapta godeffroyi*, *Hexabranchus sanguineus* (De Grave, 2000).

*Periclimenes incertus* Borradaile, 1915. Above.

*Periclimenes inornatus* Kemp, 1922 Above.
Laing Island; Davit Wreck; Wanginam reef'; Bisal Paap reef; Hansa Bay, 6-30 m; on *Actinodendron plumosum; Heteractis magnifico* (De Grave, 2000).

*Perielimenes kempi* Bruce, 1969
Hansa Bay, Laing Island; Purar Island reef; 5-10 m; on soft corals (De Grave, 2000).

*Perielimenes madreporae* Bruce, 1969
Hansa Bay, Laing Island; Duangit reef; 3-7 m; in *Pocillopora. damicornis* (De Grave, 2000).

*Periclimenes magnificus* Bruce, 1979. Above.

*Periclimenes ornatus* Bruce, 1969
Hansa Bay, Laing Island; on *Entacmaea quadricolor* (De Grave, 2000).

*Perielimenes perlneidus* Bruce, 1969
Hansa Bay, Duangit reef, 35 m; *Dendronephthea* sp. (De Grave, 2000).

*Perielimenes sarasvati* Okuno, 2002
Without precise locality (Debelius, 1999, *fide* Okuno, 2002).

*Periclimenes tenuis* Bruce, 1969
Hansa Bay, Duangit reef, 20 m; on crinoids (De Grave, 2000).

*Perielimenes venustus* Bruce, 1990. Above.

*Periclimenes* sp. cf. *venustus* Debelius, 1999
Milne Bay (Debelius, 1999).

*Perielimenes watanmae* Bruce, 1976

Hansa Bay, Laing Island, 10 m, on *Heliofungia actiniformis* (De Grave, 1998); 10 m; on *Porites* sp., *Lobophyllia hemprichii* (De Grave, 2000).

*Philarius gerlachei* (Nobili, 1905)
Hansa Bay, Laing Island, Sushi Maru Wreck; 11-15 m, in *Acropora* spp. (De Grave, 2000).

*Philarius imperialis* (Kubo, 1940)
Hansa Bay, Laing Island; Awar Wreck; 6-20 m; in *Pocillopora eydouxi, Acropora* sp. De Grave, 2000).

*Pliopontonia furtiva* Bruce, 1973
Loloata Island (Coleman, 1998).

*Pontonides asperulatus* sp. nov. Above.

*Pontonides loloata* sp. nov. Above.

*Pontoniopsis comanthi* Borradaile, 1915. Above.

*Stegopontonia commensalis* Nobili, 1906
Loloata Island (Coleman, 1998). Hansa Bay, Laing Island, 10 m, on *Diadema setosum* (De Grave, 2000).

*Thaumastocaris streptopus* Kemp. Above.

*Tuleariocaris zanzibarica* Bruce, 1967
Bougainville Island, Kieta (Bruce, 1967).

*Vir colemani* Bruce, 2003a. Above.

*Vir orientalis* (Dana, 1852)
Laing Island; Hansa Bay, 7-20 m; in *Acropora* spp. (De Grave, 2000).

*Vir philippinensis* Bruce & Svoboda, 1984. Above.

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# NOTE ON A NEW SPECIES OF *BRESILIA* (CRUSTACEA: DECAPODA: BRESILIIDAE) FROM ZANZIBAR

A.J. BRUCE

Bruce, A.J. 2005 12 31: Note on a new species of *Bresilia* (Crustacea: Decapoda: Bresiliidae) from Zanzibar. *Memoirs of the Queensland Museum* **51**(2): 385-390. Brisbane. ISSN 0079-8835.

A new species of bresilliid shrimp from Zanzibar is described and illustrated. The single specimen described is incomplete, lacking all pereiopods. It can be readily distinguished from the six previously known species of the genus and a key is provided for their identification. The record is the first for the Indian Ocean and confirms the occurrence of the genus, usually found in deep sea depths, in shallow water. ☐ *Crustacea, Caridea, Bresiliidae, Bresilia sp. nov., Zanzibar, Indian Ocean.*

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Bresiliid shrimps are of particular interest due to the persistent uncertainty of their systematic relationships. The Bresiliidae has undergone numerous re-arrangements since its original designation by Calman in 1896. It seems unlikely that its status has been finally resolved. Recently Holthuis (1993) included in the Bresilioidea only a single family, the Bresiliidae, with eleven genera, of widely varying morphology, including several recent additions from deep sea hydrothermal vents. Others are commensals of shallow water coral reef Porifera. These 11 genera have been re-distributed by Martin & Davis (2001) in the Bresiliidae, Agostocarididae, Alvinocarididae, Disciadidae and Mirocarididae. Vereshchaka (1997) suggested synonymy of the Agostocarididae with the Bresiliidae. The Mirocarididae has been synonymized with the Alvinocarididae (Komai & Segonzac, 2003). Currently the Bresiliidae, Alvinocarididae and Disciadidae are recognized. *Pseudocheles* Chace & Brown has been placed in its own monogeneric family, Pseudochelidae (De Grave & Moosa, 2004).

The Bresiliidae may now contain only the single genus *Bresilia* (Calado, et al., 2004), (although the poorly known *Encantada* Wicksten should probably also be included). Its systematic relations with other caridean remain particularly obscure. The biology of these shrimps is similarly unclear. *Bresilia* was designated by Calman (1896) for a specimen of a species of small deep water shrimp collected off the west coast of Ireland, *Bresilia atlantica*. Three further specimens were described by Kemp (1910) and one noted by Komai & Segonzac (2003). There were no further Atlantic records of this genus until Calado et al. (2004) reported *Bresilia saldanhai*, from a marine cave at a depth of 15 m, on the island of Madeira, the first report of the genus from shallow water. *Bresilia corsicana* (Forest & Cals (1997) was reported from 450m off Corsica; *B. antipodarum*; from 800m off Tasmania (Bruce, 1990b) and 770-830m off New Caledonia (Bruce, 2004a); *B. plumifera* Bruce, 1990a, from 133m, also off Tasmania, and *B. briankensleyi* Bruce, 2004b, from 750-753m from the Red Sea.

*Bresilia saldanhai* is the best known species, represented by 12 specimens, *B. atlantica* is known from 5 specimens, while *B. antipodarum* is now known from 3. *Bresilia corsicana, B. plumifera* and *B. briankensleyi* are still known only from the holotype specimens, the latter two both damaged and incomplete. No specimens of *B. atlantica* have been collected since 1907, a remarkable length of time considering the amount of benthic research that has been carried out in the northeast Atlantic over the past century. Nothing is known of their biology.

Bruce (2004b) mentioned a further species from shallow water off Zanzibar, noting that the whereabouts of the unique specimen was unknown. This is still the case, but some drawings of the specimen that I originally prepared have been located. Bruce (2004b) stated that the specimen was collected from intertidal coral reef pools. This was erroneous, the true habitat being 26 m off the reef edge. The single Zanzibar specimen here reported provides a further indication that the genus is not confined to deep waters and represents the first occurrence of

FIG. 1.*Bresilia* sp., ♂, Mnemba Island. Scale bar = 1.0mm.

this genus in the Indian Ocean and in a coral reef biotope. The annotated drawings indicate that the specimen does not belong to any of the described species, but, as a full description and a holotype specimen can not be provided, it is not formally provided with a name.

CL indicates the post-orbital carapace length.

**Bresilia** sp.
(Figs 1-3)

MATERIAL. 1♂, CL 1.25 mm, Mnemba Island, off NE Unguja, Zanzibar, reef edge, 26 m, 25 September 1995, coll. N.L. Bruce.

DESCRIPTION. Very small, slender, subcylindrical, caridean (Fig. 1). Rostrum (Fig. 2A) slender, about 5.0 times longer than proximal depth, about 0.7 of CL, straight, horizontal, acute, reaching to about distal end of intermediate segment of antennular peduncle, dorsal carina well developed, extending onto anterior carapace, with 5 teeth, first tooth distinctly postorbital, articulate, spiniform, second and third teeth similar, two smaller distal teeth acute, non-articulate; lateral carinae distinct; ventral margin sublinear, non-setose, two small acute teeth, situated close together, below fourth and fifth dorsal teeth. First dorsal rostral tooth with single slender seta immediately anteriorly. Carapace smooth, mainly glabrous, dorsal surface with 2 pairs of simple submedian gastric setae, sparse simple setae posteriorly, orbit feebly developed, inferior orbital angle not observed, antennal spine small, acute, pterygostomial angle bluntly rectangular. . Abdomen smooth, first tergite with median dorsal seta, third tergite strongly produced posteriorly, angular, with sparse submedian setae, pleura of first four segments broadly rounded, fifth bluntly angular, sixth segment about 0.75 of CL, 0.57 times longer than anterior depth, tapering slightly posteriorly, posterolateral and posteroventral angles small, acute. Telson about 0.85 of CL, with 2 pairs of small dorsal spines. Epistome (Fig. 2B) with long slender median process. Antennule without special features, distinctly exceeding rostrum, upper flagellum biramous with proximal 5 segments fused, lower ramus short. Antenna with basicerite with well developed ventrolateral tooth, carpocerite short, reaching to about half of scaphocerite length, scaphocerite well developed, lamina well exceeding rostrum, about 2.7 times longer than wide, with small distolateral tooth at about 0.8 of lateral margin length, lateral margin sublinear. Eye with well developed pigmented globular cornea, cornea about 0.2 of CL, stalk stout, width about 1.5 times corneal diameter. Mouthparts not examined. Third maxilliped endopod long and slender, basis with well developed plumose exopod. Pereiopods all missing, coxae without epipods, bases of first and second pereiopods with well developed plumose exopods; pereiopods 1-4 with pleurobranch. Fifth thoracic sternite with large acute broad median tooth, sixth and seventh each with pair of long slender submedian teeth, eighth with long tapering blunt median process. Pleopods and uropods without special features; second pleopod endopod with appendix masculina.

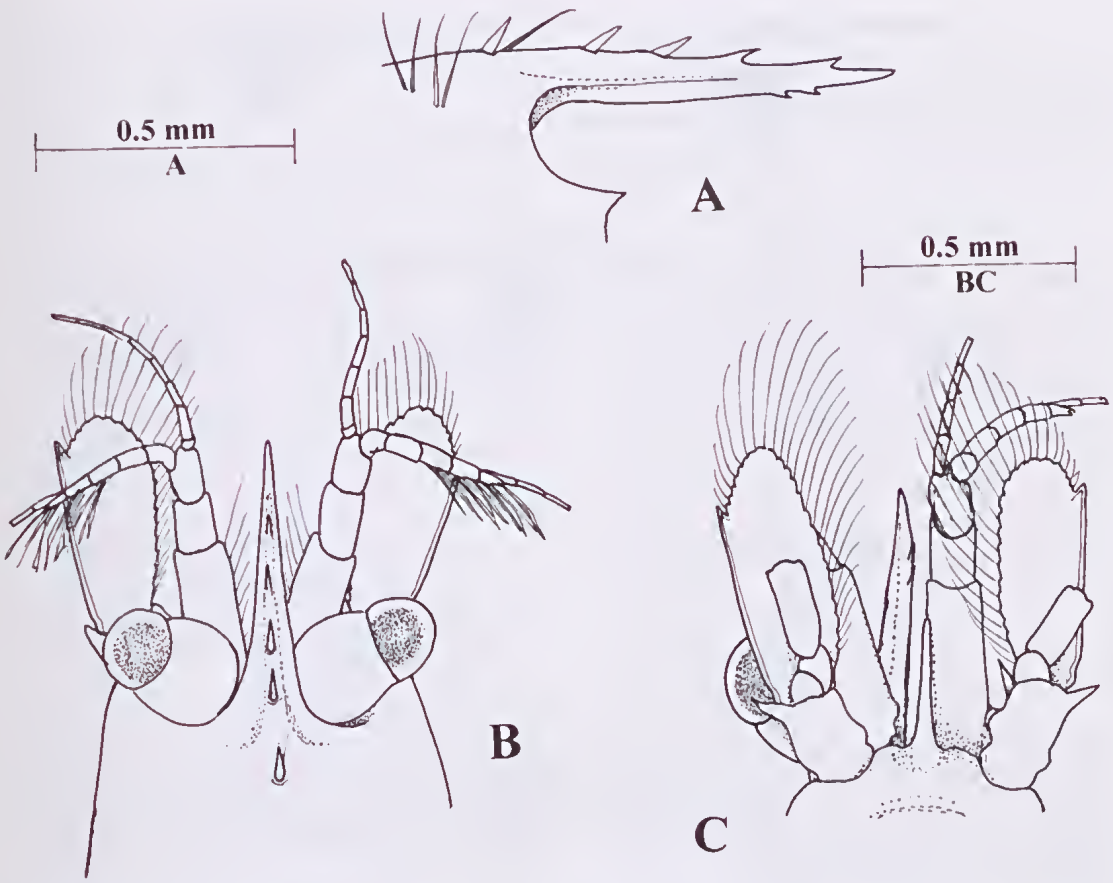


FIG. 2. *Bresilia* sp., ♂, Mnemba Island. A, rostrum. B, anterior carapace, eyes and antennal peduncles, dorsal. C, epistomal region, ventral.

SYSTEMATIC POSITION. This species may be distinguished from all other known species by its rostral dentition, 5/2, with the three articulated posterior teeth. In its incomplete state, it would be premature to assess its closest relationships. The sparse setation of the dorsal carapace and abdomen may be a further autapomorphic character but it is possible that similar setae may have been lost in the few other known specimens of this genus. This factor would not have occurred in the case of the several hand-collected specimens of *B. saldanhai* (Calado et al., 2004).

REMARKS. Although incomplete, the single specimen of *Bresilia* sp. emphasises the general morphological homogeneity of the species of *Bresilia*.

The original drawings of this specimen bear annotations suggesting re-examination of the pterygostomial angle and the posteroventral angles of the fourth and fifth pleura. This suggests that these might possibly have been acute, but probably not markedly so. Also noted was the presence of two pairs of small dorsal telson spines, but these were not shown on the drawing.

The epistomal process, first described in *B. antipodarum,* has now also been reported in *B. plumifera, B. saldanhai* and *B. briankensleyi.* It appears likely that it is a generic character, without parallel in the Caridea. It was not reported in the original description of the genus and attempts to locate and re-examine the type material in the collections of the Dublin Natural History Museum have been unsuccessful (pers. com., Julia Sigwart, 19 November 2004). The original description and partial re-descriptions of *Encantada spinoculata* (Wicksten, 1989 ; Bruce, 1990) did not report on the presence or absence of

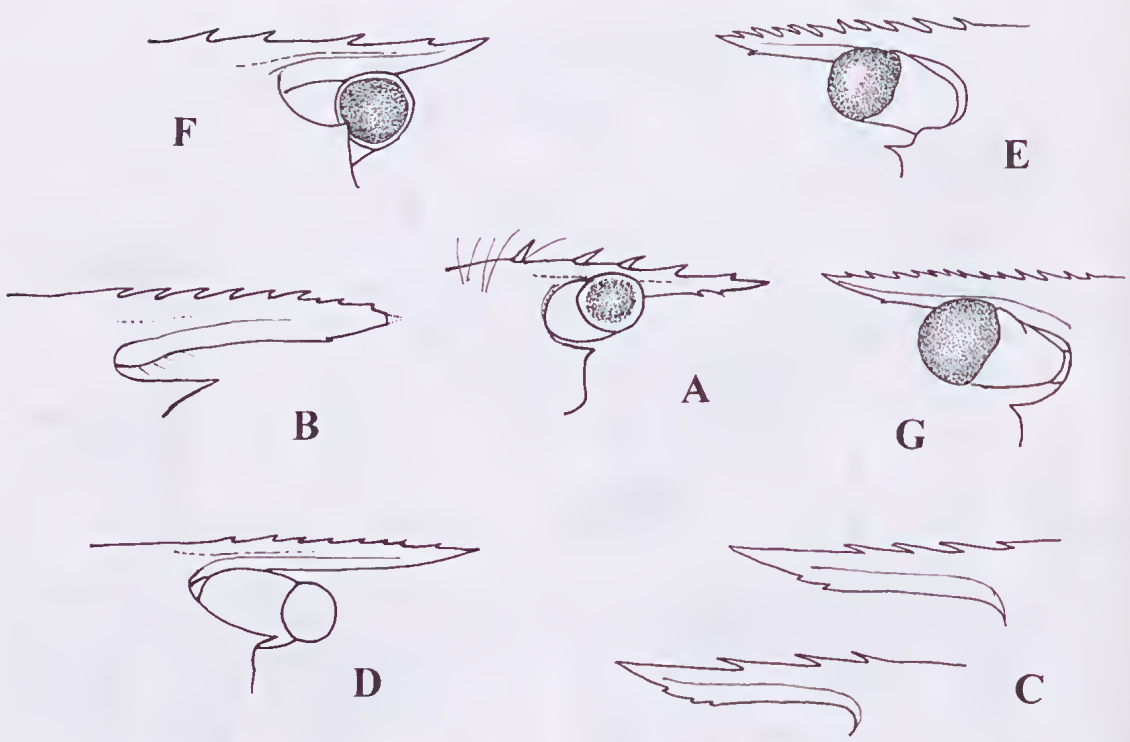


FIG. 3.*Bresilia* species, rostra, not to scale. A, *Bresilia* sp., Mnemba Island. B, *Bresilia antipodarum* Bruce (redrawn after Bruce, 1990). C, *Bresilia atlanticum* Calman, (redrawn after Calman, 1896). D, *Bresilia briankensleyi* Bruce, (redrawn after Bruce, 2004b). E, *Bresilia corsicana* Forest & Cals, (redrawn after Forest, & Cals, 1977). F, *Bresilia plumifera* Bruce, (redrawn after Bruce, 1990a). G, *Bresilia saldanhai* Calado et al. (redrawn after Calado et al., 2004).

an epistomal process. Its presence in *Encantada spinoculata* has now been confirmed, in which "it's neither as long, nor as robust as the example you have given me. It looks to be about half the length and much more delicate than the one you've illustrated (i.e., *Bresilia* sp., Fig. 2C)" (pers.com., R. Van Syoc, 21 September 2005). Its presence in *Encantada* further supports the inclusion of that genus in the Bresiliidae.

It was also not described in the original description of *B. corsicana*. This specimen is now in very poor condition and the presence or absence of the epistomal process can not be ascertained (Xinzheng Li, pers. com., 2 Nov. 2004). The specimen of *B. atlantica* noted by Komai & Segonzac (2003) is in a similar state (Xinzheng Li, pers. com., 2 Nov. 2004). The collection locality of this specimen is obscure but it was collected on 12 September 1901, from 1225-1262m depth, similar to the type material (1372m, Calman, 1896). The epistomal process has been confirmed in *B. antipodarum, B. plumifera, B. briankensleyi, B. saldanhai* and the present *Bresilia* sp.

Specimens of *Bresilia* seem particularly prone to the loss of pereiopods. The second to fifth pereiopods of *B. plumifera* are unknown, as are all pereiopods of *B. briankensleyi* and *Bresilia* sp. The holotype of *B. antipodarum* also lacked ambulatory pereiopods, but these have now been described (Bruce, 2004). The following key may facilitate the identification of pereiopod-free specimens, but in all cases careful comparison with the available descriptions should be made and confirmatory characters should be sought. The genus *Bresila* is clearly widespread, occurring in the Northeast Atlantic and western Mediterranean, the Red Sea, western Indian Ocean and western Pacific Ocean, over a wide bathymetric range, so that the collection of further new species of the genus must be considered likely.

With the re-assessment of the position of *Encantada*, the Bresilioidea now appears as follows:

Bresiliidae Calman, 1896
*Bresilia* Calman. 1896; *Encantada* Wicksten, 1989

Disciadidae Rathbun, 1902
*Discias* Rathbun, 1902; *Lucaya* Chace, 1939; *Tridiscias* Kensley, 1983

Agostocarididae Hart & Manning, 1986
*Agostocaris* Hart & Manning, 1986

Alvinocarididae Christoffersen, 1986
*Alvinocaris* Williams & Chace, 1982; *Rimicaris* Williams & Rona, 1986; *Chorocaris* Martin & Hessler, 1990; *Opaepele* Williams & Dobbs, 1995; *Mirocaria* Vereshchaka, 1997

Pseudochelidae De Grave & Moosa, 2004
*Pseudocheles* Chace & Brown, 1978

*Incertae sedis*
Kirnasia Burukovsky, 1988

## A KEY FOR THE PROVISIONAL IDENTIFICATION OF *BRESILIA* SPECIES, BASED ON ROSTRAL CHARACTERS (Fig. 2)

1. Rostral dentition 5/2, first tooth postorbital, first three teeth articulated (carapace and first and third abdominal tergites with sparse slender setae dorsally; third tergite produced, angular, fifth pleuron unarmed, telson with 2 pairs of dorsal telson spines) . . . . . *Bresilia* sp.

   Rostrum without articulated teeth (carapace and abdomen glabrous) . . . . . 2

2. Rostrum without postorbital teeth (third abdominal tergite dorsally produced, angular . . . . . 3

   Rostrum with postorbital teeth . . . . . 4

3. Rostrum slender, 0.77 of postorbital carapace length, dentition 8/0 (telson unknown) . . . . . *B. briankensleyi* Bruce, 2004

   Rostrum deeper, 0.66 of postorbital carapace length, dentition 9/1 (telson with 4 pairs of dorsal spines) . . . . . *B. antipodarum* Bruce, 1990b

4. Rostrum short, 0.31 of postorbital carapace length, first tooth markedly postorbital, second tooth slightly postorbital, dentition 4/0 (third abdominal tergite dorsally produced, angular, telson with 3+ (?) pairs of dorsal spines) . . . . . *B. plumifera* Bruce, 1990a

   Rostrum longer, first tooth slightly postorbital, ventral rostral teeth present, (third abdominal tergite dorsally gibbous) . . . . . 5

5. Rostrum 0.52 of postorbital carapace length, elevated, rostral dentition 3-4/2-3 (7 pairs of dorsal telson spines) . . . . . *B. atlantica* Calman, 1896

   Rostrum with more than five dorsal rostral teeth, horizontal, not elevated, single ventral tooth only . . . 6

6. Rostrum 0.64 of postorbital carapace length, rostral dentition 10/1 (5 pairs of dorsal telson spines) . . . . . *Bresilia corsicana* Forest and Cals, 1997

   Rostrum 0.55 of postorbital carapace length, rostral dentition 10-13/1-2 (6-7 pairs of dorsal telson spines) . . . . . *Bresilia saldanhai* Calado et al., 2004

## ACKNOWLEDGEMENTS

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# NEW DEVONIAN GASTROPODS FROM THE BROKEN RIVER AND THEIR PALAEOECOLOGY

ALEX G COOK AND ALEXANDER NÜTZEL

Cook, A. G. & Nützel, A. 2005 12 01. New Devonian gastropods from the Broken River and their palaeoecology. *Memoirs of the Queensland Museum* 51(2): 391-397. Brisbane ISSN 0079-8835.

Gastropod collections from two localities of the Givetian Papilio Mudstone were compared for species richness and faunal composition. Despite lithological similarity and same age, both localities differ strongly in their gastropod faunas, one is fairly diverse with 15 species with even richness while the other comprises four species but is strongly dominated by one species (98% of all specimens). The diverse fauna is dominated by species of the genera *Murchisonia* and *Leptoptygma*, the other by *Brokenriveria*. Up to now, nine species have been reported from the diverse fauna. Seven taxa are described, of which *Frydaeosta minuta* gen. et sp. nov., *Zliehomphalina panae* sp. nov., *Austroneilsonia yooi* sp. nov. and *Eneochlis withnalli* sp. nov are new. □ *Gastropoda, Devonian, Givetian, paleoecology, Queensland.*

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Gastropods are abundant faunal elements within the Middle Devonian platform sequences of the Graveyard Creek Subprovince, Broken River Province, north Queensland (Cook & Camilleri, 1997). Subsequent bulk collection has yielded a further seven species from the Papilio Mudstone (Givetian). The regional stratigraphy of the Graveyard Creek Subprovince was detailed by Withnall & Lang (1993) and locality data were provided by Cook & Camilleri (1997).

Material is lodged in the palaeontology collections of the Queensland Museum (QMF).

## PALAEOECOLOGICAL COMMENTS

Cook & Camilleri (1997) identified three broad gastropod communities corresponding to muddy shelf (*Brokenriveria* community), high energy clastic shelf (*Labrocuspis* community) and peri-reefal (*Murchisonia* community) environments. Detailed collection in the Papilio Mudstone has identified stark differences in faunal composition between localities, which are difficult to rationalise on sedimentological evidence. The Papilio Mudstone locality that has yielded the most diverse and abundant gastropod collection is QML1092 (Cook & Camillieri, 1997; Table 1).

A second collection (Table 1) from this locality resulted in about 1340 specimens in 13 taxa; the most numerous Givetian gastropod fauna in the Southern Hemisphere. *Bellerophon* sp. B and Platyceratoidea gen. et sp. indet. were not found again, so that the number of reported species from QML1092 is 15. It is quite normal that additional collections produce rarer species. However, it is remarkable that additional collecting also resulted in a restructuring of the recognised trophic core of the community. *Murchisonia wandovalensis* is the most common species, but it is followed by *Leptoptygma queenslandicus* that ranked fourth in Cook & Camillieri's collection. *Denayella lomandraensis* had rank two and is now fifth in abundance. So in this case the increase of known specimens by a factor of about eight resulted in a clearly different faunal composition. Apart from gastropods, this locality yields abundant brachiopods and bivalves, e.g., nuculids, solitary rugose corals and sporadically the tabulate coral *Thamnopora*. Moreover, the fauna contains rare microcrinoid calices and nautiloids.

A fauna of four gastropods in the Papilio Mudstone at QML1016 and about 3km away at QML1092 (Cook & Camilleri, 1997) is nearly monospecific at QML1016 with *Brokenriveria pharlapensis* (389 specimens) representing 98% of the fauna, while the other three species are incidental: *Denayella lomandraensis* (3 specimens), *Palaeozygopleura dodgeyi* (2 specimens), and *Geminimodosa langi* (1 specimen). Other fossils includeabundant brachiopods e.g., *Warrenella* and *Desquamatia*, nuculid bivalves, and nautiloids. Rare colonies of

massive *Alveolites* sp. and *Heliolites* sp. are associated, several tens of metres along strike, forming micro-atolls. No microcrinoid calices were recovered.

Both localities have the same lithofacies and are of same age. QML1016 is significantly south of the 'Burges Marine Valley' of Withnall & Lang (1993), negating shelf/slope as a possible ecological difference. Both faunas indicate moderately protected conditions well within the photic zone. Therefore these differences in the faunal composition are notable. It is reasonable to assume that the more diverse *Murchisonia/ Leptoptygma* community from QML1092 was under less environmental stress than the nearly monospecific *Brokenriveria*-dominated community. A particular autecology, maybe a broader tolerance towards certain environmental factors enabled *Brokenriveria* to cope with a harsher environment. Autecology in fossil gastropods is largely a subject of speculation, but fluctuation in oxygen concentration is always a reasonable guess in fine-grained deeper water environments. So maybe *Brokenriveria* was relatively tolerant to low oxygen concentrations, and the differences reflect minor variations in benthic circulation on the muddy shelf.

Table 1. Number of specimens collected from QML1092 in rank abundance order based on those made for this work.

| Taxon | This work | Cook & Camilleri |
|---|---|---|
| *Murchisonia wandovalensis* | 538 | 75 |
| *Leptoptygma queenslandicus* | 376 | 13 |
| *Austroloxa tasselli* | 162 | 22 |
| *Brokenriveria pharlapensis* | 77 | 3 |
| *Denayella lomandraensis* | 72 | 31 |
| *Austroneilsonia yooi* | 35 | |
| *Palaeozygopleura dodgevi* | 34 | 4 |
| *Frydacosta minuta* | 17 | |
| *Eucochlis withnalli* | 12 | |
| *Gemininodosa langi* | 8 | 10 |
| *Zlichomphalina panae* | 3 | |
| *Soleniscus? sp.1* | 2 | |
| *Frydacosta* sp. | 1 | |
| *Soleniscus? sp. 2* | 1 | |
| Platyceratoidea indet. | | 1 |

## SYSTEMATIC PALAEONTOLOGY

Subclass ARCHAEOGASTROPODA Thiele, 1925
Family SINUOPEIDAE Wenz, 1938
Subfamily SINUOPEINAE Wenz, 1938

### **Frydacosta** gen. nov.

ETYMOLOGY. For Jiři Frýda (Prague).

TYPE SPECIES. *Frydacosta minuta* sp.nov.

DIAGNOSIS. Rotelliform, low-spired sinuopeid with strong axial ribs.

REMARKS. Most sinuopeids lack the strong axial ribs of this new genus which is placed in the subfamily due to the wide central sinus. *Naticasinus* Pan & Erwin, 2002 from the Late Permian of Guangxi is similar but has fewer ribs and is slightly higher spired. *Frydacosta* is lower spired that *Sinuopea* Ulrich and *Sellenima* Perner. *Horiostomella* Perner is phaneromphalus, unlike this new genus.

### **Frydacosta minuta** sp. nov. (Fig. 1 A-M)

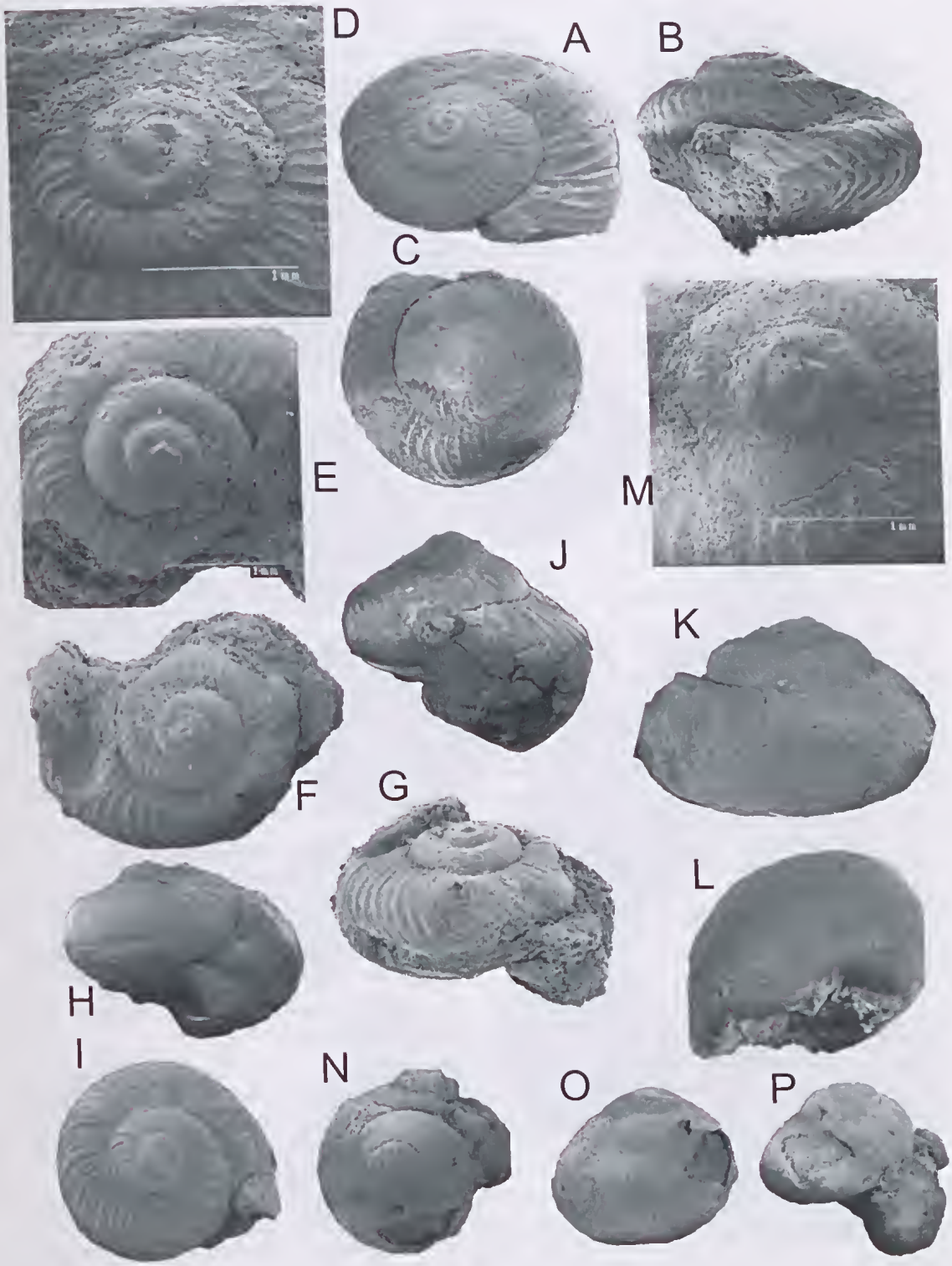
DIAGNOSIS. As for genus.

MATERIAL. Holotype QMF43371, Paratypes QMF 43372-43374, QMF41897-QMF41908 from QML1092.

ETYMOLOGY. Latin, *minuta,* small.

DESCRIPTION. Shell rotelliform, low-spired, whorls convex, sutures impressed, periphery just below mid-whorl; teleoconch whorls with numerous axial ribs, strongly prosocline forming wide, deep sinus just below periphery; ribs continue onto base; whorl profile unequally convex; upper whorl face nearly flat at suture, extending at low angle to a strongly convex mid-whorl; lower whorl surface nearly flat; upper whorl surface more convex in early whorls; aperture not well-preserved, simple, subcircular; base in early whorls anomphalous, in later whorls cryptomphalous; protoconch corroded, seemingly simple, paucispiral.

FIG. 1 (facing). A-M, *Frydacosta minuta* gen. et sp. nov. A-E, Holotype QMF43371. A-C, oblique apical, side and apical views, x15. D, E, oblique and apical view of protoconch, x25. F-H, Paratype QMF43372, apical, side and apertural view, x15. I-M, Paratype QMF43377. I-L apical, apertural, side and basal views, x15. M, apical view of protoconch. N-P, *Frydacosta* sp. QMF43375, apical, side and apertural views, x15.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**Frydacosta** sp.
(Fig. 1N-P)

MATERIAL. QMF43377 from QML1092.

DESCRIPTION. Like *F. minuta* but more high-spired, sinus much wider and deeper; ribs a little finer especially on base; about 4.5 whorls, 5.2mm wide, 3.8mm high, base cryptomhalous, convex; whorl profile rounded; upper whorl meets sutures at about 20°; periphery at mid-whorl; sinus just below mid-whorl; sutures moderately impressed.

Family EOTOMARIIDAE Wenz, 1938
Subfamily EOTOMARIINAE Wenz, 1938

**Zlichomphalina** Frýda, 1998

TYPE SPECIES. *Pleurotomaria (Ptychomphalina) texta* Barrande in Perner, 1907.

**Zlichomphalina panae** sp. nov.
(Fig. 2A-E)

ETMYOLOGY. For Dr Pan HuaZhang (Nanjing).

MATERIAL HOLOTYPE QMF 43378; PARATYPES QMF43379-43380 from QML1092.

DIAGNOSIS: Lenticular shell form.

DESCRIPTION. Shell small, lenticular, low-spired; up to 8.3 mm wide, 5.5 mm high; sutures weakly impressed; periphery just at the midwhorl suture; slit at lower suture; upper whorl face gently sloping, till it meets the wide slit which is bordered by cords and the lower suture; slit occupies the lower one third of the upper whorl face. Upper whorl face with numerous distinct prosocline and curved axial threads, whorl base convex base minutely phaner-omphalous, bearing numerous ribs; ribs deflected backwards at selenizone. Upper cord bordering selenizone making an angulation; first two whorls corroded without visible ornament; aperture apparently rounded

REMARKS. *Zlichomphalina* was erected for Early Devonian eotomariines with a small gap between the suture and the lower bounding cord of the selenizone which is relatively high on the shell. This Queensland material extends the generic range to the Middle Devonian. It differs from the types species in its lenticular shell form.

Subfamily NEILSONIINAE Knight, 1956

**Austroneilsonia** Sabattini, 1975

TYPE SPECIES. *Austroneilsonia argentina* Sabattini, 1975 from the Late Carboniferous of Argentina.

REMARKS. Two portmanteau neilsoniins characterise this typically post-Devonian subfamily, *Peruvispira* Chronic and *Neilsonia* Thomas. Their origin is unclear, but given the presence of neilsoniines within the Middle Devonian (*Peruvispira churkini* Blodgett, 1992 and herein) there is a long geological history to the subfamily. The confusion between *Neilsonia* and *Peruvisprira* is common, with the subtlety of axial ornamentation and selenizone position confusing many (eg, Qiao, 1983). *Austroneilsonia* Sabatini, 1975 was erected for neilsoniins present on the Late Carboniferous to Permian Gondwanan faunas, which possessed coarse collabral ornament, but lacked subsutural nodes. Traditionally these coarsely ornamented taxa had been placed within *Peruvispira* Chronic 1949. This material before us presents a particular problem, a coarsely ornamented neilsoniin which predates all the exemplar members of the family. Its selenizone position and lack of nodes prevent assignment to *Neilsonia* and its coarse ornament preclude *Peruvispira*, which would be restricted to those with growth lines only. We accommodate the material within *Austroneilsonia* Sabatini on the basis of the coarse collabral ornament which is continuous across the whorl face.
Included species are *Peruvispira gundyensis* Yoo, 1988 and *P. churkini* Blodgett, 1992.

**Austroneilsonia yooi** sp. nov.
(Fig. 2F-S)

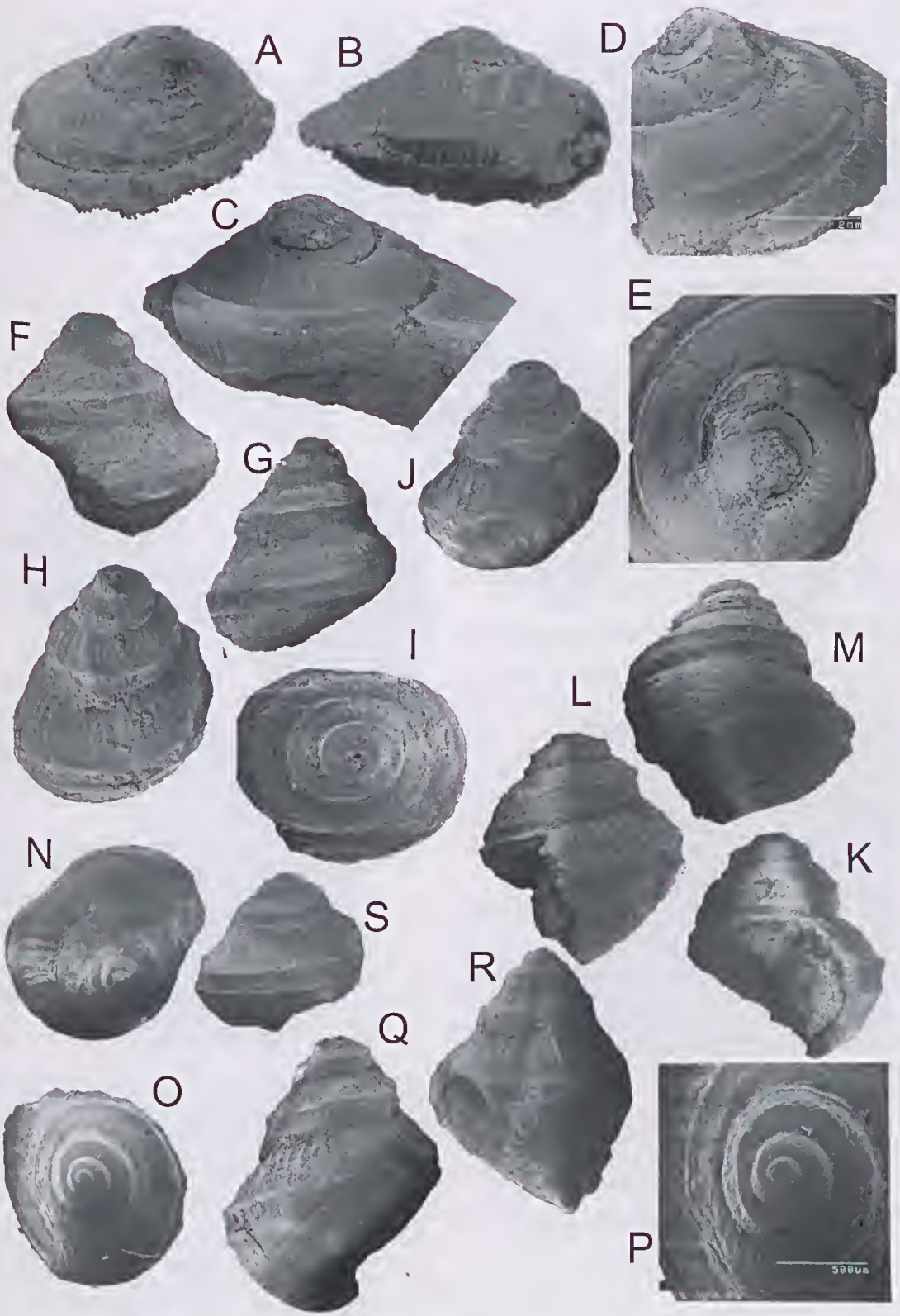
ETYMOLOGY. For E. K. Yoo

DIAGNOSIS. *Austroneilsonia* with coarse widely spaced collabral ornament,

MATERIAL. Holotype QMF 42064, Paratypes QMF 42065-42092 from QML1092

DESCRIPTION. Shell small, turbiniform, relatively high-spired of up to 5 whorls, up to 3.2mm high, 2.1mm wide at base; whorl profile angular: selenizone at mid-whorl periphery;

FIG. 2 (facing). A-E, *Zlichomphalina panae* gen. et sp. nov. Holotype QMF43378. A,B, oblique, side views, x10. C, side view, x15. D, oblique view, x20. E, apical view, x20. F-S, *Austroneilsonia yooi* sp. nov. F-G, Paratype QMF42066 side view, x15. H-J, Holotype QMF42064 oblique, apical, side views, x15. K-N, Paratype QMF42065. K, apertural view, x15. L, side view, x10. M, oblique basal view, x15. L, apical view, x10. O, S Paratype QMF42067 apical, side views, x12. P-R, Paratype QMF42093 side views, x15, apical view, x30.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sutures impressed; whorls embrace just below lower border of selenizone; selenizone bordered by two spiral threads; upper whorl face meets suture at about 45°; upper whorl face with numerous axial threads; collabral threads prosocline, curving backward towards selenizone; base rounded, anomphalous, with numerous collabral threads; aperture simple round; apex flattened, protoconch corroded.

REMARKS. This material differs from the type species in its more widely spaced collabral ornament. It differs from *A. gundyensis* (Yoo) by the lack of strong deflection of the cords as they approach the selenizone.

Family ELASMONEMATIDAE Knight, 1956

**Eucochlis** Knight, 1933
**Eucochlis withnalli** sp. nov.
(Fig. 3 A-G)

ETYMOLOGY. For Ian W. Withnall for his contribution to north Queensland geology.

MATERIAL. Holotype QMF41909, paratypes QMF41910-42920 all from QML1092.

DIAGNOSIS. Small, turbiniform, anomphalous.

DESCRIPTION. Shell small, turbiniform, with at least four whorls, up to 3.5mm high and 3mm wide; teleoconch whorls convex with numerous sharp, strongly prosocline curving ribs, more than 20 per whorl, continuing onto base; sutures impressed; base round, convex, anomphalous; aperture not well-preserved, seemingly simple, subcircular with reflexed inner lip; protoconch corroded, seemingly simple, paucispiral.

REMARKS. This species closely resembles the type, *E.perminuta* Knight, 1933 from the Pennsylvanian of North America, however it is not cyrtoconoid and has no minute umbilicus. This is the first report of *Eucochlis* from the Devonian. *Eucochlis australis* Yoo, 1988 from the Tournaisian Dangarfield Formation (NSW) is minutely phaneromphalous and has more inflated whorls.

Subclass CAENOGASTROPODA Cox, 1959
Family SUBULITIDAE Lindstrom, 1884
Subfamily SOLENISCINAE Wenz, 1938

**Soleniscus** Meek & Worthen, 1861
**Soleniscus?** sp. 1
(Fig 3H)

MATERIAL. QMF43381, QMF43382, from QML1092.

DESCRIPTION. Shell fusiform, up to 7.3 mm high, 5.4mm wide; last whorl at least one half of shell height; sutures moderately impressed; whorl face meeting suture at about 30°; no obvious growth lines; periphery just below midwhorl; whorls convex bearing no visible ornament.

REMARKS. We were unable to identify a columellar fold, the generic assignment is uncertain, and the specimens were too worn for specific identification. The subulitid *Leptoptygma queenslandicus* Cook & Camilleri, 1997, which is abundant at this locality, has a much more robust and squat shell form.

**Soleniscus?** sp. 2
(Fig 3 I-K)

MATERIAL. QMF42063 from QML1092.

DESCRIPTION. Shell small, fusiform, about five whorls present, 5.8mm high, 3.1 mm wide; last whorl occupies about two thirds of shell height; whorls embrace at periphery; whorls convex with numerous fine axial threads; sutures shallow; aperture elongated, with anterior notch, twisted so that a weak columellar fold is present.

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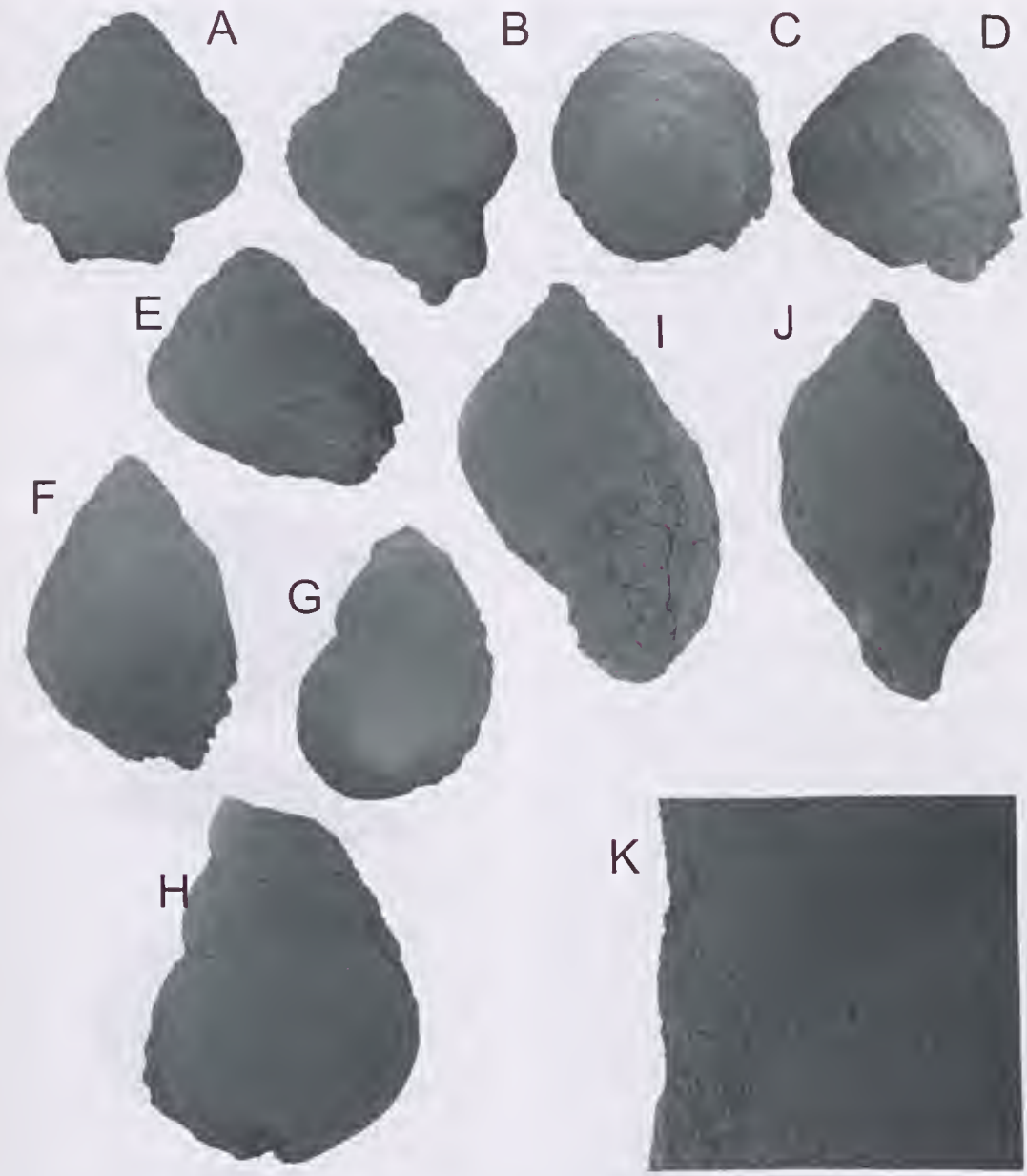


FIG. 3. A-G, *Eucochlis withnalli* sp. nov. A-C, Holotype QMF41909, side, apieal views x10. D,E, Paratype QMF41910 side, apertural views x10. F,G, Paratype QMF41911 (distorted), apertural, side views x10. H, *Solensicus*? sp. 1, QMF43381. I-K, *Solensicus?* sp. 2, QMF42063. I,J, apertural, side views x10. K, detail of ornament x40.

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**FOSSIL LIMPET FROM THE CRETACEOUS OF NORTH QUEENSLAND.** *Memoirs of the Queensland Museum 51(2): 398. 2005-* Fossil limpets have a very poor pre-Tertiary record within Australia with *Siphonaria samwelli* Etheridge, 1892, from the Early Cretaceous of north Queensland the only binomially ascribed taxon and two other in very open nomenclature from the Late Cretaceous of Western Australia (Darragh & Kendrick, 1994). Collection of material by Mr Paul Tierney, from the Coffin Hill Member of the Gilbert River Formation, has provided a large number of limpet specimens allowing review of Etheridge's species. Material is derived from Mount Angus near Croydon, NCQ, where the Coffin Hill Member of the Gilbert River Fmn overlies Proterozoic granitoids forming small silica-rich duricrusts atop mesas. These units are interpreted to represent nearshore sandy bottom and reworked rocky shore communities based on their gross sedimentology and proximity to basin margin and basement. A rich mollusc fauna with sparse brachiopods is known from this locality. Burger (1986) suggested a Hauterivian- Barremian age for the Coffin Hill Mbr in well holes BMR Gilberton 2, Richmond 3 and GSQ Hughenden 7 placing it within the *Foraminisporus wonthaggiensis* and *Murospora florida* spore pollen zones corresponding to his cycles 5a-b. Dinoflagellate studies of Oosting (2004) placed the unit within the lower Aptian which more comfortably accommodates the macrofauna present in the Croydon area.

Suborder PATELLINA von Ihering, 1876
Superfamily PATELLOIDEA Rafinesque, 1815
Family ACMAEIDAE Carpenter, 1857
**Scurriopsis** Gemmellaro, 1879

*Type species. S. neumayri*, from the Jurassic of Sicily.

**Scurriopsis samwelli** (Etheridge, 1892)

*Siphonaria samwelli* Etheridge in Jack & Etheridge, 1892: 573, pl. 42, fig. 9.

*Material examined.* Holotype GSQF1335. QMF44659-QMF44671 from Mount Angus, NE of Croydon, NQ. All are external moulds.

*Description.* Shell conical, bilaterally symmetrical, imperforate, elliptical in outline, wider posteriorly; apex towards anterior, one third distance along shell length; up to 24 mm wide, 33 mm long and 9 mm high. Ornament of two orders of radial ribs commencing on the apex extending to form a crenulate margin; four or five stronger ribs on the posterior shell, two or three on the anterior a little weaker; second order ribs only slightly stronger than most fine concentric growth lines which form by intersection of a reticulate network. Growth lines mostly fine, but sporadic and irregularly spaced coarser rugae. Stronger in some specimens than others. Slit absent. Protoconch unknown, muscle scars unknown.

*Remarks.* The imperforate shell shown by ornament on the apex places the material in the Pattellina. Ornament and apex placement suggests affinifites to the Acmaeidae and the height to length ratio suggest placement in *Scurriopsis*. Type taxa of constituent subgenera lack the strong ornament of the present material, but other species demonstrate such ornament. *Scurriopsis* (*S.*) *aptiana* Kase 1984 (p.50, pl. 2, figs 1-3) has such ornament but has a more centrally located apex. The material is reminiscent of *Patella* (s.l.) *miyakoensis* Kase 1984 (p. 54 pl. 2, figs 4-5) from the Lower Cretaceous (Aptian)Hiraiga Fmn, of Japan, which has similar ornament but a more central apex.

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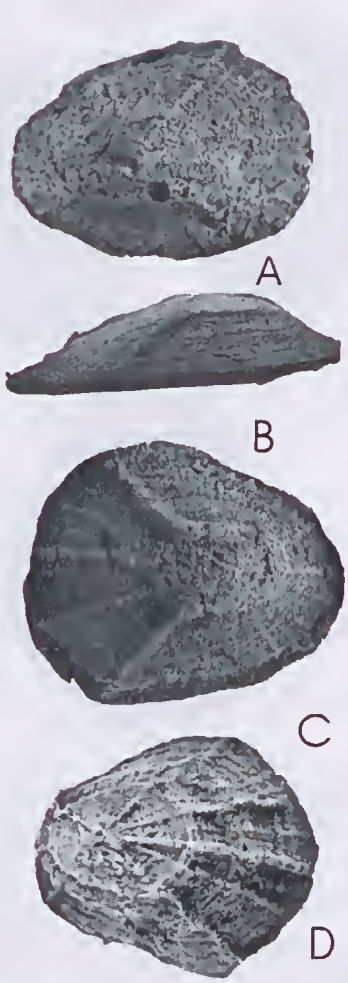


Fig.1. *Scurriopsis samwelli* (Etheridge, 1892). A. QMF44659, apical view x 1.5. B,C. QMF44671 side and apical views x1.5. D, QMF44673, apical view x 1.5.

# *CHIROPSALMUS MACULATUS* SP. NOV., A CUBOMEDUSA FROM THE GREAT BARRIER REEF

PAUL F. S. CORNELIUS, PETER J. FENNER & RUSSELL HORE

Cornelius, P.F.S., Fenner, P.J. & Hore, R. 2005 12 01: *Chiropsalmus maculatus* sp. nov., a cubomedusa from the Great Barrier Reef. *Memoirs of the Queensland Museum* **51**(2): 399-405. Brisbane. ISSN 0079-8835.

A large cubomedusa, *Chiropsalmus maculatus* sp. nov., is described from the only known specimen, observed and collected live near the outer edge of the Great Barrier Reef. It is distinctive in lacking a 'palm' to what is a palmate, compound pedalium in other known chirodropids, and in having conspicuous, deeply corrugated subumbrellar muscle-fields. It is unique among known cubomedusae in having a pigmented exumbrellar epidermis. Much of the surface was covered in life by more than 40 discrete, sub-circular, patches of colour, and the base of each pedalium was encircled by a fine line of pigment. Some of the patches were arranged in a loose pattern, and there was a regular circle of unpigmented epidermis surrounding each rhopalium, both suggesting strongly that the coloration was genotypic and not due to a pathogen or other cause external to the animal. ☐ *Cnidaria, cubomedusae, chirodropids, venomous, box jellyfish, Great Barrier Reef.*

*Paul F. S. Cornelius, 51 Green Court Road, Crockenhill, Swanley Kent, BR8 8HF, United Kingdom; Peter J. Fenner, PO Box 3080, North Mackay, Queensland 4740; Russell Hore, Reef Biosearch, Port Douglas, Queensland 4871, Australia; 27 June 2004.*

A single cubomedusa was collected in May 1997, in latitude 16° S, some 40 km off the coast of NE Queensland, near the outer edge of the Great Barrier Reef. The specimen was c. 150 mm high, and its bell was conspicuously spotted with brown patches, whereas other known cubomedusae almost entirely lack bell coloration. It is described here as *Chiropsalmus maculatus* sp. nov. (Fig. 1). The area attracts much attention from divers and snorkellers. Many of them will be aware of the extremely venomous *Chironex fleckeri* Southcott, 1956, endemic in the region and similar in general appearance to the species described here. Since the new species has not been reported before it may be genuinely rare in the area. Its occurrence may be related to the passage through the area a few weeks earlier of Cyclone Justin, following which a teleost fish (*Lethrinus*), typically found off the continental shelf, occurred in coastal waters, suggesting a similar deepwater origin of the newly described medusa. Although just one specimen is known, its features are so distinctive that its recognition as previously undescribed is justified.

## MATERIALS AND METHODS

We were reluctant to dissect the unique specimen. In fact, within two years in formaldehyde solution it had become so stiff and brittle that further detailed study might have damaged it in ways unnecessary to provisionally define the species. Detailed study of rhopalia, velarial canals, sinuses, nematocysts and some other features will best await further specimens.

The word pedalium is applied in cubomedusan literature to two dissimilar structures. In one of the two generally recognised cubomedusan families, the Carybdeidae, at the base of each tentacle is a thickened or otherwise demarcated region termed the pedalium. Such pedalia are inserted in four groups, one at each lower corner of the bell, but each individual pedalium is there attached directly to the lower edge of the bell. In the Chirodropidae, however, the tentacles on each corner are inserted essentially around the edge of (in most species) a palm-shaped structure which has also been termed a pedalium. In the present account, a distinction is made where necessary by use of the terms individual pedalium for the first and compound pedalium for the second. Other terminology follows Williamson et al. (1996) and Mianzan & Cornelius (1999) which included a glossary.

It is not known if the new species is venomous to Man. However, in view of the extreme virulence of some chirodropids great caution should be exercised with live specimens. The species is one of the larger chirodropids and, if venomous to Man, its large size might well result in massive, harmful envenomation.

FIG. 1. *Chiropsalmus maculatus* sp. nov., drawn from video sequence, photographs of live animal and preserved specimen. Note that the tentacles are partially contracted. The shape of the rhopalial slit in life was invisible in the video sequence of the specimen swimming prior to collection, and distorted in the preserved specimen. The blank rhopalial area, shown, may, therefore, represent the normal appearance in life, but confirmation is needed. Bell height 150 mm.

## SYSTEMATICS

Phylum CNIDARIA
Subphylum MEDUSOZOA Petersen
Class CUBOZOA Werner
Order CUBOMEDUSAE Werner
Family CHIRODROPIDAE Haeckel

### **Chiropsalmus** L. Agassiz, 1862

REMARKS. Generic divisions in the Chirodropidae are traditionally based on the form of the gonads and subumbrellar saccules, which at sexual maturity are processes of varied shape hanging down into the subumbrellar space. The saccules are regarded as infertile in *Chiropsalmus* but bear the gonad tissue in the single species assigned to *Chironex*. Since the specimen of the present species had neither gonads nor saccules, generic assignment cannot be made on these features. It is, therefore, referred only provisionally to *Chiropsalmus*. This action is preferred over introduction of a monotypic genus because such a genus might fall when fertile material is found.

At present the Chirodropidae comprises *Chiropsalmus* Agassiz, 1862, *Chirodropus* Haeckel, 1880, and *Chironex* Southcott, 1956, of which the last is considered monotypic. The introduction of monotypic or even small genera, closely resembling previously recognised ones, in any family, needs firm justification based on appropriate distinction. Hence some generic revision may be needed in this family since gonad structure alone has been employed. Some account should be taken of generic divisions in other cubo- and scyphomedusae, because in the latter, at least, intrageneric variation in gonad structure is seldom taken as justification for generic separation. Although we suggest that generic revision among chirodropids might be useful, it is inappropriate in the present account of one specimen.

An unusual constraint on the generic assignment of species in the highly venomous Chirodropidae should be stressed here. The need for easy and rapid access to stored medical data by clinicians urgently treating potentially fatal sting cases should perhaps pragmatically over-ride zoological convention. *Chironex fleckeri* is extremely dangerous to Man, some envenomations causing death within a few minutes (Williamson et al., 1996). It is also a common species along tropical Australian coasts and along those of several tropical countries to the north. Thus it will be useful in information retrieval in an emergency, that the genus name should be retained only for the one so-far known extremely venomous species, *Chironex fleckeri*. Whether or not *Chiropsalmus maculatus* sp. nov. is venomous to Man is unknown. But if it proves harmless, future generic revisers will hopefully agree that regardless of anatomy it should not be referred to *Chironex*. Though one or more *Chiropsalmus* species (depending on taxonomic view) are harmful, they are less so than the one species of *Chironex*, and some are quite harmless. Since *Chironex* can kill in less than five minutes, depending partly on envenomation intensity, the appearance in literature-searching during an emergency of unhelpful references to harmless species might contribute to clinical disaster. The point is emphasised here to forestall over-zealous nomenclatural revision, perhaps materially inhibiting clinical practice.

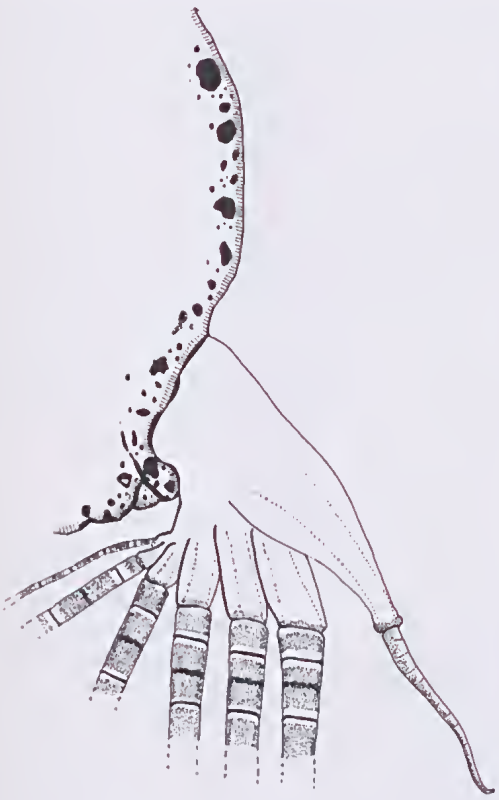

FIG. 2. *Chiropsalmus maculatus* sp. nov. Single compound-pedalium in side view with associated individual tentacle bases. Length of upper segment of compound pedalium 60 mm.

**Chiropsalmus maculatus** sp. nov.
(Figs 1-6)

MATERIAL. HOLOTYPE QMG316989: Just inside Outer Barrier Reef, NE Queensland, 43 km off mainland, 15° 59.050'S, 145° 49.294'E, 2 May 1997, within 5m of surface, coll. R. Hore. A 23-second underwater video sequence was taken of the living animal before collection, and is deposited with the type specimen. There was a substantial, permanent, illuminated Man-made structure in the vicinity, but the specimen was noticed in daylight. The specimen could not be fixed for several hours, and subsequently proved notably brittle and fragile.

DESCRIPTION. A solid chirodropid with conspicuous vertical fluted ridges at corners and massive pedalial bases jutting out prominently from lowermost 1/5 of bell (Fig. 1); irregular sub-circular brown patches over most of epidermis, arranged quasi-regularly in lines and in other patterns, but not present in a hyaline circular patch surrounding each rhopalium. Composite pedalia unlike those of *Chironex fleckeri* in not being palmate, the tentacles being inserted contiguously (Fig. 3B,C).

Bell 150 mm high; in life seeming spherical in side view, apex slightly rounded to flat, cuboid in plan view; corners of bell grooved from top to within 15 mm of pedalium, deepest (9 mm) aborally; sides of bell with two further grooves, c. 4 mm deep, straight from within 50 mm of upper edge to level of rhopalium where deflect inwards, passing within 2 mm of rhopalial niche, then extending to velarium but not meeting it. Exumbrellar surface and mesogloea transparent in life, internal structures visible through it where exumbrellar pigment absent. Jelly maximum thickness 10 mm in perradius, 20 mm in interradius; flexible in life but bending only slightly during swimming; firm after preservation in formaldehyde solution.

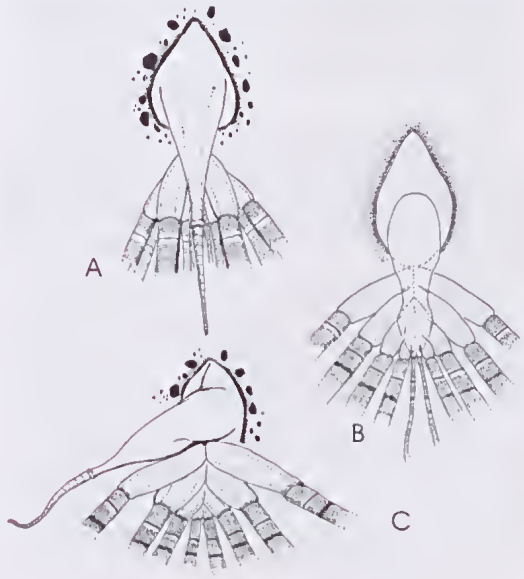


FIG. 3. *Chiropsalmus maculatus* sp. nov. A, B, single compound-pedalium in plan view from outside of specimen. Left upper, A, in natural position. Left lower, B, with the unpaired outer section pulled to reader's left. Right middle, C, same from inside to show contiguous bases of the paired tentacle bases. In C the puny, unpaired outer tentacle is not visible since the view is from the inside; and two small, paired, probably young tentacles are shown in the mid-line.

FIG. 4. *Chiropsalmus maculatus* sp. nov., part of subumbrellar surface of holotype. Note the deeply folded muscle-fields and the gastric cirri. Scale in mm.

Velarium thin; width about 1/4 bell aperture; when extended during bell contraction, slightly tapering below; edge seemingly frilled but even; connected to subumbrellar surface by a frenulum in each of the 4 perradial planes; velarial canals not discerned.

Rhopalial niche large, entrance slit probably shallowly curved in life but shape unclear from specimen and photographic material, 6-9 mm wide, closed and distorted in preserved specimen and apparently closed in video sequence; surrounding epidermis slightly puckered several hours after collection, possibly smooth in life, colourless; lips flush with outer surface; rhopalium (in preserved specimen) totally enclosed within closed niche and not examined.

*Pedalia and tentacles.* Each compound pedalium (Figs 2, 3) inserted on lowermost 1/5 of bell, its area of attachment inverted heart-shaped, pointed above; slightly tapering distally; symmetrical about mid-line, and without palmate central region as in *Chironex*; comprising a large triangular outer portion bearing single tentacle, and two mirror-image flanking portions apparently fused together in mid-line; outer portion in side view elongate-triangular, projecting conspicuously clear of rest of pedalium, bending slightly (as though hinged) at mid-point of upper surface on each power-stroke of bell; bearing single, narrow, short and puny tentacle, its length in life approximately half bell diameter, and trailing outside main cluster of tentacles; two inner portions each comprising 5-(probably)7 thick, almost cylindrical, pedalial 'fingers', flattened laterally, inserted closely together with opposite and adjacent pedalial bases contiguous or nearly so. Each tentacle moderately thick, hollow, tapering distally; perhaps typically 15 per bell corner (7x2 plus one puny outer) but in present specimen up to 5x2 plus puny outer and also two small presumed tentacle bulbs; outermost one on each compound pedalium unpaired and circular in section, rest paired and flat in section, tapering gradually to point; new tentacles developing from inner side of pedalium.

Subumbrellar surface of bell (Fig. 4) in each inter-rhopalar radius having large field of horizontal muscle-folds, occupying nearly whole height of bell, up to 50 mm across, widest about halfway up bell; about 70 folds in each muscle field. Other, much smaller, vertically-orientated muscle fields near margin of subumbrella.

*Gastric system.* Manubrium a wide square tube, attached by substantial suspensoria to within 40 mm of mouth; approximately 140 mm long (measured from subumbrella surface) but probably extensile; with convoluted internal surface (this visible from outside) from top to lowest level of suspensoria.

Mouth lips tortuous, slightly thicker than manubrial tissue.

Gastric cirri numerous, up to c. 5 mm long in preserved specimen, finely tapered distally, in conspicuous phacelli (Fig. 4).

Radial and ring sinuses, 'rose-thorn corniculum' not discerned through dimly translucent tissue, even with light behind and after injection of (labile) dye into lumen of one compound pedalial base; but detailed exploration not undertaken owing to fragility and uniqueness of specimen.

Gonads and subumbrellar saccules not identified. Possibly convoluted tissue outside manubrium was gonadial, specimen may be infertile.

*Colour and colour pattern.* Epidermis with numerous large irregular patches, approximately circular to oval, each c. 10 mm diameter, and numerous scattered, smaller, spots; orange-brown in life, seeming dark chocolate at c. 10 m

FIG. 5. *Chiropsalmus maculatus* sp. nov. Typical banding pattern of a partially contracted main tentacle. Note that variation within the single specimen examined, and intraspecific variation in other chirodropids, suggest that the banding pattern should not be taken as consistent in the species, pending further information.

depth in the sea; some of oval patches twice as long as wide. Several ragged vertical rows of coloured patches per side, those in some rows larger than in others. On each side approximately 24 large patches and 400 of all sizes; c. 35 medium-sized ones clustered in centre of each side; distribution of all spots and larger patches densest towards velarium; remaining spots c. 330 per side, more irregular in outline, some tendency to cluster as 'satellites' of the largest ones. Exumbrellar grooves orange/brown. Elastic tissue of vertical corners of subumbrella reported bright purple before preservation (RH). Compound pedalia colourless, but base of each narrowly rimmed orange-brown. Tentacles (Fig. 5) in life banded purple and white, the bands 1-6 mm wide; losing colour in formaldehyde solution; typically with the narrowest, darkest bands flanked each side by slightly wider pale band (in triplets of light-dark-light), with much longer section of intermediate colour intensity between, but this, the commonest arrangement, inconstant in places; the bands typically identical in position on adjacent tentacles but this uniformity decreasing distally (from video and from photographs of live specimen by R.H.)

DIMENSIONS. Bell height 150 mm (top of bell to base of velarium), maximum width 160 mm. Length of compound pedalium 60 mm. Velarium 27 mm wide. Distance from rhopalar niche to edge of velarium 25 mm; niche height 17 mm, diameter 20 mm. Tentacle diameter up to 10 mm; length extended in life 1.0-1.2 m (from video, maybe longer if completely undisturbed), 300 mm when contracted after preservation in formaldehyde solution. In preserved specimen, the 4 small, outer tentacles (one per pedalial group) 4 mm wide basally, 40 mm long, tapering gradually to point; larger tentacles up to 135 mm long (as contracted in preservative), 10 mm wide basally tapering to 3 mm wide at truncate tip.

STING. No unequivocal information. Following collection the single specimen was kept in sea water in a small bucket at ambient tropical daytime temperature for 5 hrs, after which it failed either to sting, or adhere to, the hand and forearm of an incautious volunteer. This gives no firm indication of its possible virulence, since *C. fleckeri* can lose its capacity to sting in such temperatures (P.J.F.).

REMARKS. In *Chiropsalmus maculatus* sp. nov. the individual tentacles are contiguous basally on the compound pedalium, and there is no 'palm' separating them as in the palmate compound pedalia of other chirodropids. *C. maculatus* sp. nov. differs additionally from *Chirouex fleckeri* in having brown spots on the exumbrella and a brown line around the base of each pedalium, the epidermis of *C. fleckeri* and of other large chirodropids being essentially colourless; in the billowing of the bell during swimming, recognised by RH as differing notably from the more rigid appearance of the bell in *C. fleckeri*; and in the coloration of the tentacles (Fig. 5). The general colour pattern of these, of bands of varied width arranged in a semi-regular but varying pattern, recalls that in *Chiropsalmus quadrumanus*. It differs markedly from that in *C. fleckeri*, in which there are typically wide, dark bands separated by narrow, pale bands, there being typically bands of two widths and two colours. In all chirodropids with coloured bands on the tentacles, the contraction of part or all of a tentacle reduces the widths of the bands and distorts the pattern. In the new species the rhopalia are noticeably each surrounded by a clear region devoid of pigment, as though

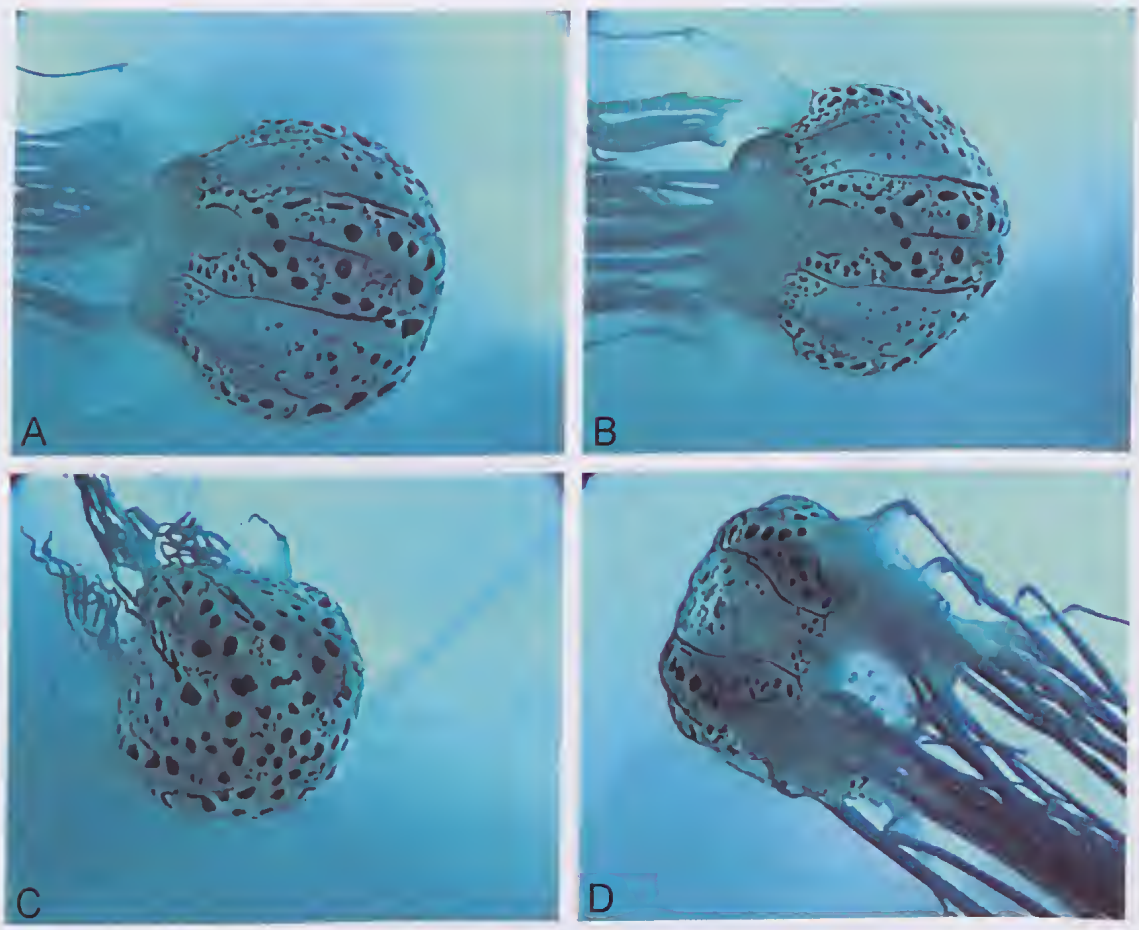


FIG. 6. *Chiropsalmus maculatus* sp. nov. Details of holotype after collection. Stills captured from a DVD sequence prepared from underwater video. Water depth was not recorded, but the colours are probably distorted towards the blue through attenuation. The specimen had been the subject of attention, and the tentacles are probably contracted and contorted: in the related *C. palmatus*, in undisturbed individuals the tentacles stream out straight and parallel with one another and are more attenuate. A-B, side views at (A) and near (B) end of bell contraction during swimming; note fully distended velarium, the round profile of the bell, the shape of the compound pedalium with the outer section supporting a single, puny, unpaired tentacle; the pale rhopalar discs between the pedalium bases; the transparent, thin jelly in the rhopalar radii; and the banded tentacles. C, aboral ('top') view; note somewhat square section with thicker jelly at the corners, and the prominent outward projection of the outer branch of the pedalium. D, oral view; note transparency of the thin jelly in the rhopalar radius, visible through the wide velarial aperture; and the pedalia.

enabling the rhopalial photoreceptors to better detect light. In this species the unpaired outermost tentacle on each compound pedalium is puny in comparison with the others, being much shorter and narrower, whereas in *C. fleckeri* it is approximately equal in length and width to the other tentacles, and in *C. quadrumanus* it is between the two in relative size. Finally, in the new species the folds in the inter-rhopalar muscle-fields are much deeper than in other chirodropids (Fig. 4).

## CONCLUSIONS

Little can be said about the so-far unique occurrence of this species since there is little indication of how it got to the collection locality. The species should be regarded by those handling

it as possibly very dangerous to Man, like other large chirodropids, until proved otherwise.

## ACKNOWLEDGEMENTS

We are grateful to Ann Alexander, University of Wales, Bangor, U.K., for executing the pen-and-ink drawings, and for detailed discussion of the anatomy of the species with PFSC; to Robin Cook, of Reef Biosearch, for taking the excellent underwater video sequence of the holotype specimen; and to Phil Crabb of the Photographic Studio, The Natural History Museum, London, for Figure 4. We are grateful to Graeme Harper, Director of the Centre for Creative and Performing Arts, University of Wales, Bangor, for discussing the video sequence with PFSC and Ann Alexander, and for its enhanced transfer to DVD format for detailed viewing. RH collected the specimen, and provided the still photographs of it in life and soon after death.

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**FIRST RECORD OF FOSSIL FRESHWATER GASTROPODS WITHIN THE WINTON FORMATION.** *Memoirs of the Queensland Museum 51(2):406. 2005:-* The Winton Formation is a mid Cretaceous (latest Albian to Cenomannian) terrestrial deposit which covers significant parts of the central west of Queensland and is the uppermost unit of the Eromanga Basin sequence. It contains a diverse flora (McLoughlin et al., 1995), sporadic terrestrial and aquatic vertebrate fauna and associated ichnofauna (Thulborn & Wade, 1984; Dettman et al., 1992), and freshwater bivalves (Hocknull, 2000). No gastropods have been previously recorded in this unit. Freshwater and estuarine gastropods are known in the Aptian (Etheridge, 1902; Kear et al., 2003), and early Albian (Hamilton-Bruce et al., 2002) of the Great Artesian Superbasin.

These two poorly preserved gastropod specimens are noteworthy due to their rarity and as the first record of gastropods within the Winton Formation. The material is preserved as part of silicified peat accumulations commonly referred to as "forest floor".

Family THIARIDAE Troschel, 1857
**Melanoides** Olivier, 1804
**Melanoides** sp. indet. (Fig 1)

*Material.* QMF49451, QMF49452, lowermost Winton Formation, Wanora Stn, NW of Winton.
*Description.* Shell turriculate, 14.9 mm high, 6.1 mm wide, spire angle approx 15°; no apex or protoconch preserved. Suture impressed situated well below mid whorl, whorls flattened, whorl face gently convex bearing regular costae. Aperture not preserved.
*Remarks.* A coarser non-cancellate ornament and less elongated whorl profile is noted on both specimens than that of *Melanoides godthelpi* Hamilton-Bruce et al., 2004. Affinity to the genus is indicated by the obvious ornamentation and shell shape.

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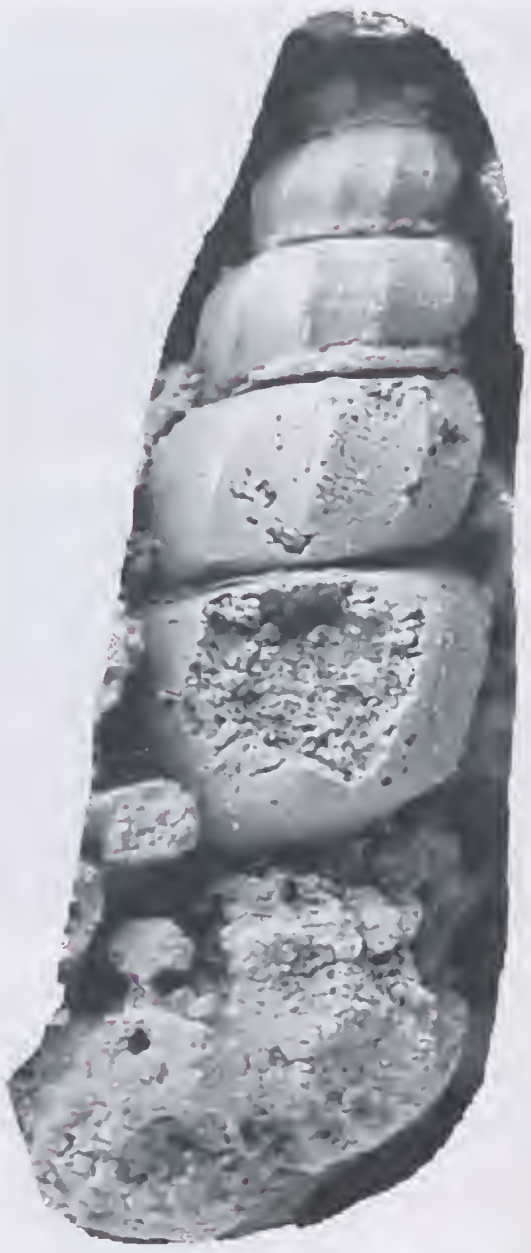

Fig 1. *Melanoides* sp.. Side view QMF49451, specimen 15mm high.

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# THE PENAEOIDEA OF THE NORFANZ CRUISE

W. DALL

Dall, W. 2005 12 01: The Penaeoidea (Crustacea: Decapoda) of the NORFANZ Cruise. *Memoirs of the Queensland Museum* **51**(2): 407-422. Brisbane. ISSN 0079-8835.

The NORFANZ Cruise was a collaboration between Australian, New Zealand and French scientific organisations to investigate the biodiversity of the Norfolk Ridge and Lord Howe Rise benthic communities. Most of the stations occupied during this cruise (89%) were in water deeper than 300m, with 40% in depths exceeding 1000m. Accordingly the penaeoid fauna consisted mostly of deeper water species and were collected at 73 stations by trawls and sledges. All five families of the Penaeoidea were represented by 21 species, the Aristeidae being predominant, mostly *Aristeus mabahissae, Aristaeomorpha foliacea, Austropenaeus nitidus*, plus *Aristeus virilis, Aristaeopsis edwardsianus, Hepomadus tener*. Benthesicymidae: *Benthesicymus investigatoris, B. howensis , Gennadas gilchristi, G. kempi*. Solenoceridae: *Gordonella kensleyi, Hadropenaeus lucasii, Haliporoides sibogae, Hymenopenaeus methalli, H. neptunus, H. obliquirostris, Solenocera comata*. Penaeidae: *Metapenaeus velutina, Funchalia villosa*. Sicyoniidae: *Sicyonia inflexa, S. truncata*. Details of location and depth of each species and the geographical range are given. As *Gordonella kensleyi* males were collected for the first time, a complete description can now be given. Examination of males of *Benthesicymus urinator howensis* indicate it should be raised to specific rank. □ *Penaeoidea, NORFANZ Cruise, Norfolk Ridge, Lord Howe Rise.*

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*20 June 2005*

The NORFANZ Cruise was planned to investigate the marine biodiversity of the Norfolk Ridge and Lord Howe Rise seamount and slope communities. It was a joint investigation between Australian, New Zealand and French scientific organisations, using the New Zealand R.V. Tangaroa. The scientific crew was made up from a rotation of personnel from various institutions: New Zealand (Te Papa and NIWA), Australia (CSIRO, Australian Museum, Museum Victoria, NT Museum, Queensland Museum, and University of Tasmania), France (IRD, MNHN), USA (California Acad. Sciences).

The Norfolk Ridge and Lord Howe Rise are prominent bathymetric features of the Tasman Sea between Australia and New Zealand. They are considered to be part of the old coastline of Gondwanaland. Parts of these ridges rise to chains of seamounts and plateaus 200–1000m below the surface. Previous limited investigations have found that some localities support rich and diverse communities, characterised by high levels of endemism.

The objectives of the Cruise were to sample communities and document the marine diversity from 14 seamounts and slopes to at least 1500 m. depth. The Cruise began on 9 May, 2003 with the first station at 34°06'S, 171°39'E to the west of Three Kings Islands (near the northern tip of the North Island of New Zealand) and proceeded north along the Norfolk Ridge to 26°22'S, 167°01'E; turned west on a course of about 250° to Middleton Reef, 29°14'S, 159°06'E; south to Lord Howe Island, 31°45'S, 159°19'E; then set an easterly course to the West Norfolk Ridge, 34°12'S, 163°21'E, finally turning southeasterly along the West Norfolk Ridge approximately parallel to the original track, finishing on 7 June, 2003. A total of 168 stations were occupied, including 15 CTD and 9 photographic stations (Clark et al., 2003). Williams & Gowlett-Holmes (2003) provided a progress report.

Only 73 of the 168 stations yielded identifiable penaeoids (Table 1.). Most of these (34%) were collected by the ORH trawl; 26% by the Sherman epibenthic sledge; 19% by the "Rateatcher" trawl, 15% by the beam trawl and the remainder by the NIWA sled and midwater trawl. The last was disappointing as a number of penaeoids have been shown to be epibethic or bathypelagic, and thus likely to be caught by this device (Griffiths & Brandt, 1983; Kikuchi & Nemoto, 1991).

All 5 families of the Penaeoidea represented by 21 species were collected, but the Aristeidae were predominant. Nearly all have been recorded in Australian waters (Dall, 1999, 2001). Species distributions are discussed below.

## SYSTEMATICS

### Superfamily PENAEOIDEA
### Family ARISTEIDAE Wood-Mason, 1891

*Aristaeina* Wood-Mason, 1891: 278.
*Aristaeinae* Alcock, 1901: 27; Ramadan, 1938: 36; Kubo, 1949: 193.
*Aristeinae* Bouvier, 1908: 13; Balss, 1957: 1516; Crosnier, 1978:14.
*Aristeidae* Crosnier, 1978:14; Burkenroad, 1983: 281; De Freitas, 1985: 3 ; Pérez Farfante & Kensley, 1997: 175; Dall, 2001.
*Aristaeidae* Grey et al., 1983: 13, 14; Dall et al., 1990:58.

For diagnoses and keys see Pérez Farfante & Kensley, 1997 and Dall, 2001.

#### **Aristaeomorpha foliacea** (Risso, 1827)

*Penaeus foliacea* Risso, 1827: 69pl.2, fig.6; H. Milne Edwards, 1837: 418; Miers, 1878: 307.
*Aristeus rostridentatus* Bate, 1881: 189; 1888: 317, pl. 51.
*Aristaeamorpha foliacea* (see Crosnier, 1978 for bibliography to 1978); Crosnier, 1984: 54, figs 23, 24; 1985: 861; 1989: 42; 1994b, 369; Hayashi, 1983b: 280, fig. 53; Grey et al., 1983: 46, pl. 1; de Freitas, 1985: 16, fig.11-7; Liu & Zhong, 1986: 33, figs 12, 13; Yu & Chan, 1986; Kensley et al., 1987: 279; Dall, 2001: 412, fig. 2.

MATERIAL. Station 2, 3♀, 12, 28, 33mm; Station 3, ♂, 30mm; Station 27, ♂, 34mm, ♀, 37mm; Station 28, ♀, 30mm; Station 43, ♀, 37mm; Station 80, ♀, 17mm; Station 81, 2♂, 35mm, 4♀, 25-49mm; Station 86, 3 juveniles 10-14mm; Station 89, 3 juv. 7-12mm, 2♂, 23-26mm, 5♀, 25-46mm; Station 94, ♀, 19.5mm; Station 108, 5♂, 25-38mm, 10♀, 14-42mm; Station 140mm, ♀, 40mm; Station 159, 10♂, 23-27mm, 10♀, 25-43mm.

REMARKS. 66 specimens were collected over most of the area sampled, at depths of 110-987m, 177m deeper than the maximum recorded range. This species is one of the most widely distributed of the Aristeidae, ranging from the West Pacific, around Australia, the Indian and Atlantic Oceans and the Mediterranean Sea. The present records fill a gap between New Caledonia and Australia.

#### **Aristaeopsis edwardsiana** (Johnson, 1867)

*Penaeus Edwardsianus* Johnson, 1867: 897 [part].
*Aristeus Edwardsianus* Miers, 1878: 308 [part].
*Aristeus caralinus* Bate, 1888: 32, fig. 10.
*Aristeus splendens* Richard, 1900: 89; 1903: 67,70,71.
*Aristaeopsis Edwardsiana* Wood-Mason, 1891: 283, figs 8, 9; 1892: figs. 1-2; Alcock, 1899: 74.
*Aristaeapsis edwardsiana* Alcock & Anderson, 1894: 147; Pérez Farfante & Kensley, 1997: 175, pl.36, fig. 7; Dall, 2001: 413, fig. 3.
*Plesiapenaeus edwardsianus* Faxon, 1895: 189 (for full synonomy to 1974 see Crosnier, 1978 ); Kensley et al., 1987: 281; Hayashi, 1983c: 268, fig.59; Crosnier, 1985: 863; 1994b: 369; de Freitas, 1985: 20, figs 2-9; Liu & Zhong, 1986: 43, fig. 17; Grey et al., 1983: 38, pl. 2.

MATERIAL. Station 67, ♀, 92mm; Station 94, ♀, 19.5mm; Station 95, ♀, 29mm.

REMARKS. This species appears regularly in deepwater trawls off eastern Australia, and is of minor commercial importance off Madagascar (Crosnier, 1978). As the recorded depth range is 200-1850m, Station 67 at 72-82m is exceptional. The species prefers muddy substrates (Dall, 2001), which may explain its sparseness in the present collections. It is cosmopolitan.

#### **Aristeus mabahissae** Ramadan, 1938

*Aristeus mabahissae* Ramadan, 1938: 43, figs 2b, 3b, 4a-c; Crosnier, 1978: 65, figs 25c, 26c-f; 1985: 863; 1994: 369; Hayashi, 1983a: 190, figs 49, 50; Liu & Zhong, 1986: 44, fig. 18; Komai, 1993: 22 ; Dall, 2001: 415, fig. 4A.

MATERIAL. Station 3, ♀, 43mm; Station 16, 2♂, 34mm, ♀, 47mm; Station 33, ♂, 35mm, 3♀, 51mm; Station 63, 2♀, 36, 41mm; Station 73, 3♂, 25, 32, 35; Station 74, 5♀, 48-53mm; Station 80, 6♂, 16-31mm, 10♀, 23-45mm; Station 81, ♂, 24mm, 19♀, 18-40mm; Station 90, 3♂, 32-54mm, 3♀, 40-51mm; Station 92, ♂, 32mm, 3♀, 44-51mm; Station 93, 2♀ 39-41mm; Station 94, 9 juv.9-12mm; Station 95, ♂, 27, 6♀, 40-51mm; Station 96, ♂, 31mm, 6♀, 33-50mm; Station 101, 6♀, 41-62mm; Station 103, 5♀, 35-62mm; Station 114m, 2♂, 30,31mm, 6♀, 25-70mm; Station 119, 2♂, 19-34mm; 6♀, 20-49mm; Station 123, 5♂, 26-43mm, 9♀, 19-48mm; Station 128, 8♀, 37-52mm; Station 140, 4♀, 11-41mm; Station 141, 2♀, 22,23mm; Station 146, ♂, 33mm, 7♀, 39-52mm; Station 147, 5♂, 16-32mm, 4♀, 28-45mm; Station 151, 4♀, 35-47mm; Station 155, 3♂, 30-31mm, 5♀, 41-50mm; Station 156, 4♀, 43-51mm; Station 159, 15♀, 18-45mm; Station 160, 2♀, 46, 53mm; Station 166, ♀, 8.5mm.

REMARKS. Although the largest collection of penaeoids on this Cruise, this species is sparse in the northern part of the Cruise area, more frequent on the Lord Howe Rise, and most numerous on the West Norfolk Ridge. It was trawled at depths between 800-1460m, thus exceeding the known depth range (500-1100m) at seven stations. *A. mabahissae* has been recorded from the Australian east and west coasts, Madagascar, Maldive Islands, Indonesia, South China Sea, Japan, Wallis Islands (Dall, 2001).

Doubts have been raised about the identity of this species by A. Crosnier (pers. comm.). The glabrous species of *Aristeus* are closely similar, difficult to separate and prior to Crosnier (1978), depended on relative lengths of pereopod segments for separation. Crosnier (1978, 1984, 1994b) showed that the number of photophores on the pereopods, particularly the fifth, are constant within a narrow range for each species. Unfortunately, the photophores cannot be seen in old or poorly preserved specimens, i.e. the types of *A. semidentus, A. antennatus* and *A. mabahissae*.

Much depends on the identifications made by Crosnier (1978). He compared his material with the types of *A. semidentatus* and *A. mabahissae* in the Natural History Museum, London and considered that they matched closely. Unfortunately, he had only four specimens of *A. semidentatus*, but from the data he provided (Crosnier, 1978) they appear to be very consistent. Recently Crosnier (unpubl.) searched, without success, for this species around the locality where the type specimens were found (Kermadec Islands). This search included the vicinity of New Caledonia, Vanuatu and Solomon Islands, as well as material from the NORFANZ Cruise. The latter had most *A. mabahissae* features of the pereopods (numbers of photophores and ratios of length of carpus/length of merus) with the exception of the carpus/merus ratio of the fifth pereopods, which was within the *A. semidentatus* range for the NORFANZ and New Caledonia material.

A further sample of 28 specimens, mostly female, 20-60 mm carapace length, from the NORFANZ collection show a range of photophores 7-12, mean 10.5, on the carpus of the fifth pereopod, and 8-12, mean 10.3, on the propodus, consistent with those *A. mabahissae* from various localities examined by Crosnier (unpubl.) and by Dall (2001) for Australian specimens. However, the carpus length/merus length ratio of the fifth pereopods ranged 1.03–1.43 suggesting that this ratio is not a reliable feature by itself for separating *A. mabahissae* from *A. semidentatus*.

### Aristeus virilis (Bate, 1881)

*Hemipenaeus virilis*, Bate, 1881:187; 1888:303, pl. 44, fig.4.
*Aristeus tomentosus*, Bate, 1881: 189; 1888: 307, pl. 49, figs 2,3, pl. 50.
*Hemipenaeus virilis*, Bate, 1888: 303, pl. 44, fig. 4.
*Aristaeus virilis*, Faxon, 1895: 196; Alcock, 1901: 30; Kubo, 1949: 194, figs 1, 6, 8, 13, 14,19, 23, 36, 44, 65, 69, 72, 78, 85, 86.
*Aristeus virilis*, Bouvier, 1908: 70; de Man, 1911: 6, 27; de Man, 1913: pl. 2, fig. 6; Ramadan, 1938: 39; Okada et al., 1966: 140, 141, 151, pl. 1, fig..3; Crosnier, 1978: 61, figs 25a,b, 26a,b; 1984: 21; 1985: 861; 1989: 42; 1994a: 352; Hayashi, 1983a: 190, figs 51, 52c,d; de Freitas, 1985: 3, fig. 11-1; Liu & Zhong, 1986: 37, fig. 14; Yu & Chan, 1986; Kensley et al., 1987: 281; Dall, 2001: 416, fig. 4B.

MATERIAL. Station 43, ♀, 17mm (damaged).

REMARKS. Recorded as the commonest of Australian penaeoids (Dall, 2001), but apparently rare in the NORFANZ area. Known range: South Africa, Madagascar, Andaman Islands, Indonesia, around Australia, New Caledonia, New Hebrides, Wallis Islands, South China Sea, Philippines, Japan.

### Austropenaeus nitidus (Barnard, 1947)

*Plesiopenaeus nitidus* Barnard, 1947: 383; 1950: 622: Crosnier, 1978: 89; Kikuchi & Nemoto, 1986: 52.
*Austropenaeus nitidus* Dall, 2001: 417, fig. 5.

MATERIAL: Station 47, 9♀, 31-39mm; Station 66, ♀, 17mm; Station 72, 2♂, 25,26mm, 20♀, 33-39mm; Station 73, 5♂; Station 77, ♀, 33mm; Station 90, 2♂, 21, 24mm, 6♀, 29-34mm; Station 91, 2♂, 21, 23mm, ♀, 30mm, 4 juveniles; Station 92, 4♀, 28-37mm; Station 92, ♂ 22mm, 5♀, 28-37mm; Station 101, 4♀, 33-39mm; Station 103, 5♀, 29-42mm; Station 121, ♂, 26mm, ♀, 23mm; Station 142, 3♀, 26-38mm; Station 145, ♀, 16mm; Station 146, 8♂, 18-23mm, 11♀, 15-25mm; Station 150, ♂, 22mm; Station 151, 2 juveniles; Station 155, ♂, 22mm; Station 156, 6♂, 24-26mm, 11♀, 18-38mm; Station 158, 6 juveniles 10-18mm; Station 160, 2♂, 18-27mm, 4♀, 23-27mm; Station 163, 2♀, 17-21mm.

REMARKS. This is the largest collection of this species so far recorded. Depth range was 565 – 1530m, all but one station below 1000m; seven of these exceeded the maximum published depth of 1300m. The geographical range falls well within the limits of 26°S to approx. 40°S (Dall, 2001), who disputes its reported occurence in the North Pacific at 22° N (Kikuchi & Nemoto, 1986). Otherwise *Austropenaeus nitidus* appears to be a Southern Hemisphere species ranging from the south Atlantic Ocean, off Cape of Good Hope and Natal, Amsterdam and St. Paul Islands, south Indian Ocean, south and east Australia, Lord Howe Rise and Norfolk Ridge. It is likely to occur around the North Island of New Zealand and to the east, depending on bottom topography.

### Hepomadus tener Smith, 1884

*Hepomadus tener* Smith, 1884:409, pl. 9, figs 7,8; 1887; Bouvier, 1908:57, pl.1, fig.5, pl.13, figs 1-12; Burkenroad, 1936: 86; Ramadan, 1938:55; Roberts & Pequegnat, 1970, 43, fig.3; Pequegnat & Roberts, 1971:9; Pérez Farfante, 1973: 442, figs 1-8; Crosnier, 1985: 860; 1994: 369; Dall, 2001: 419, fig. 7.
*Hepomadus tener?* Wood-Mason, 1891: 189.
*Aristaeus (Hepomadus) tener?* Alcock, 1901: 42.
*Hepomadus glacialis* Milne Edwards & Bouvier, 1909: 194, figs 13-19, pl.1, fig.3.

MATERIAL. Station 47, ♂, 41mm, ♀, 49mm

REMARKS. Collected at 1530-1934m; as the depth range is 765-5400m (Dall, 2001), a large part of its habitat may not have been reached on this Cruise. It nowhere appears to be common. Its known range is Zanzibar, Madagascar, Réunion, Bay of Bengal, NW Australia, Wallis Islands, W. and E. Atlantic Ocean.

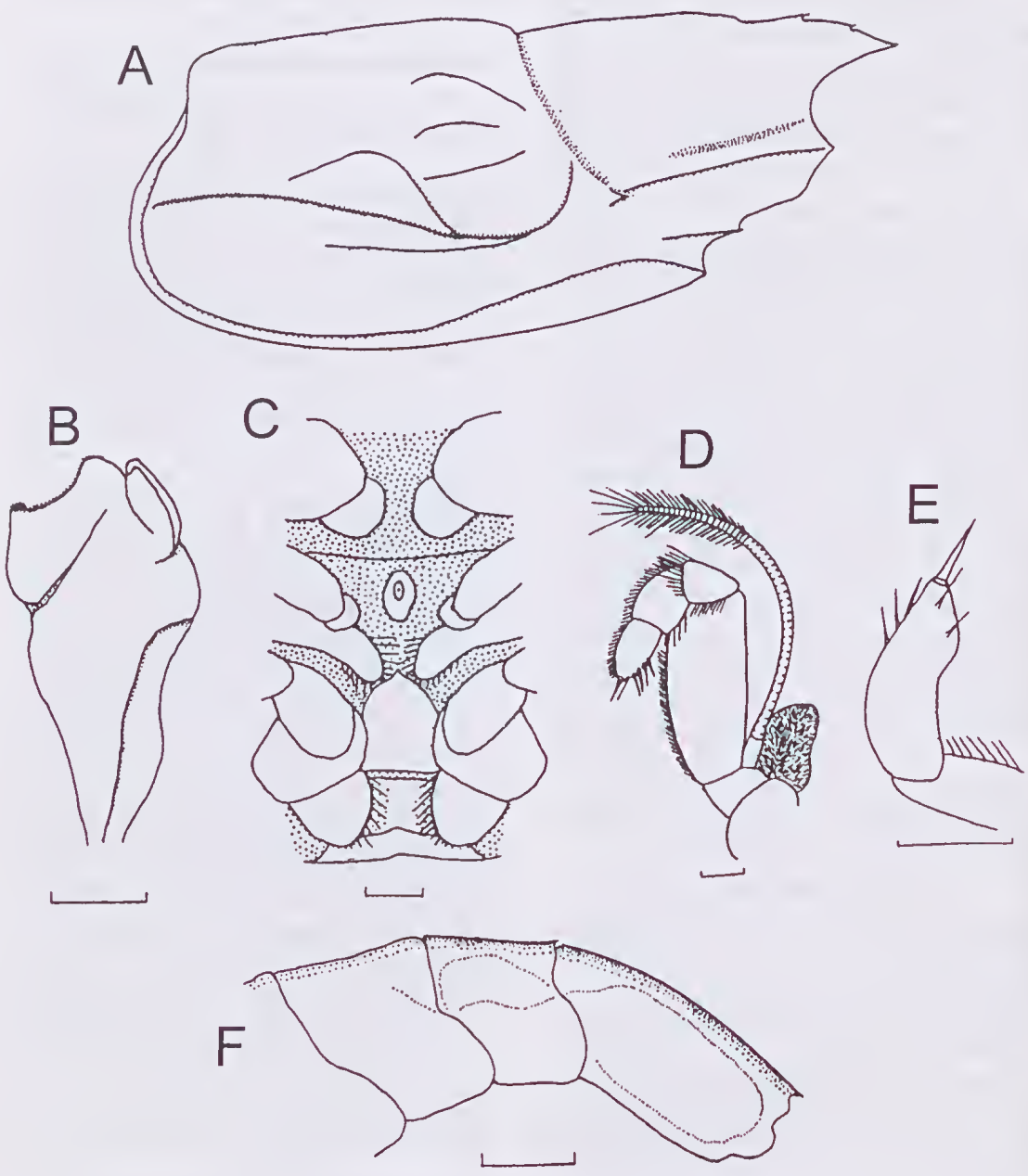


FIG. 1. *Benthesicymus howensis* Dall, 2001. ♀ holotype, 22 mm, AM P40648, Lord Howe rise, 28°44'S, 161°54'E, 1325m. A, carapace; C, thelycum; D, maxilliped 2; E, maxilliped 3, dactyl; NORFANZ Cruise, Stn. 74, 32°26'S, 161°45'E, 1171-1259m, B, ♂, 24 mm, right half petasma, anterior view; NORFANZ Cruise, Stn. 160, 34°59', 169°30', 1735m, F, ♀, 21mm, abdominal somites 4-6. Scale bars = 1mm, except F = 5mm. A, C, D, E, are from Dall, 2001.

## Family BENTHESICYMIDAE Wood-Mason, 1891

*Benthesicymina* Wood-Mason, 1891: 286.
*Benthesicymae* Bouvier, 1908, 33: 16; Burkenroad, 1936: 15; Anderson & Lindner, 1943: 290; Balss, 1957: 1517; Tirmizi, 1960: 321; Roberts & Pequegnat, 1970: 32.
*Benthesicyminae* Crosnier, 1978:14; Hayashi, 1983d: 36.
*Benthesicymidae* Pérez Farfante & Kensley, 1987: 56.

For diagnoses and keys see Pérez Farfante & Kensley, 1997 and Dall, 2001.

### **Benthesicymus investigatoris** Alcock & Anderson, 1899

*Benthesicymus investigatoris* Alcock & Anderson, 1899a: 282; 1899b, pl.41, fig.2; Alcock 1901: 44; Rathbun, 1906: 906; Balss, 1927: 247, fig.1; Burkenroad, 1936: 49; Anderson & Lindner, 1943: 298; Crosnier, 1978: 21, pls 7c,d, 8c,d, 9, 10; 1984: 20; 1985: 857; 1989: 41; 1994a: 351; 1994b: 368; Itayashi, 1983d: 440, fig. 61; Kikuchi & Nemoto, 1991: 88, figs 16,17; Dall, 2001: 427, fig. 12.
*Benthesicymus investigatori,* Borradaile, 1910: 258.
*Benthesicymus Investigatoris,* de Man, 1911:5,14; 1913, pl. 1, fig. 1.

MATERIAL. Station 47, 2♀19mm, 1 juvenile, 7mm; Station 78, 7 juveniles 13-17mm; Station 80, ♂, 14mm; Station 93, juvenile 7mm; Station 94, 40 small juveniles; Station 96, 2♂, 21mm, 5F (damaged, approx.22mm); Station 101, 5♀ 17-28mm; Station 114, 2♂, 18-21mm, 2♀ 18-20mm; Station 120, juvenile 6mm; Station 123, 3♀ 17-21mm; Station 129, ♀ 22mm; Station146, 2♂, 17-19, 6♀ 19-23mm; Station 151, ♂, 17mm; Station 155, 2♀ 21, 22mm; Station 156, 2♂, 19mm, 3♀ 21-23mm; Station 163, ♀ 18mm; Station 167, 4♂, 25mm, 9♀ 18-21mm+10 damaged.

REMARKS. This is one of the commonest *Benthesicymus* species, one trawl off NE Queensland yielding 150 specimens (Dall, 2001). It has been recorded throughout the Indo-West Pacific from the east coast of Africa, through the Indian Ocean to Hawaii and the Wallis Islands, including the NW and E coasts of Australia, Lord Howe Rise, Norfolk Ridge, Indonesia, Philippines, Japan.

### **Benthesicymus howensis** Dall, 2001 (Fig. 1)

*Benthesicymus urinator howensis* Dall, 2001: 428, fig. 13.

MATERIAL. Station 71, 2♀ 23, 28mm; Station 74, 4♂ 21-25mm, 4♀ 18-23mm; Station103, 3♂ 15-24mm, 4♀ 23-25mm; Station 120, 2♂ 25-29mm, ♀ 28mm; Station 121, 3♂ 11♀ all damaged; Station 160, ♂, 19mm, 4♀ 20-23mm; Station 163, ♂ 26mm; Station 168, ♂ 24mm.

DIAGNOSIS. Integument soft and thin, carapace often damaged; rostrum reaching the eye, with two fairly prominent dorsal teeth, sometimes with third small tooth or indications thereof; posterior tooth behind margin of carapace. Antennal and hepatic spines present; branchiostegal spine prominent, situated on margin of carapace with short carina. Cervical sulcus deep, notching mid-dorsum and with lower branch continuous with branchiocardiac sulcus; branchiocardiac carina prominent; postcervical sulcus obscure, marginal carina well developed. Abdomen without postero-median spine on somite 4; without distinct spine on somite 5 in about half of specimens, the remaining half with small spine; somites 5 and 6 dorsally carinate ; sixth somite more than twice length of fifth; a complex of feeble lateral carinae and sulci on somites 5 and 6 (Fig. 1F). Merus of second maxilliped expanded, length/width ratio 2.4 (Fig. 1D); dactyl of third maxilliped broadest below its mid-point, tapering distally with one spine at the tip (Fig. 1E). Petasma leaf-like, with short dorsomedian lobule occupying about one third total length of the petasma, distally bluntly pointed, with small rounded projection on the lateral corner; ventrolateral lobule at right angles to the ventromedian lobule, with its lateral margin slightly thickened (Fig. 1B). Thelyeum with prominent swelling on the sternite of 5th pereopods, anterior end bluntly pointed; small pointed projection on the 4th sternite (Fig. 1C).

REMARKS. Dall (2001) did not feel justified in erecting a new species on the basis of two females, one of which was damaged, and instead erected the sub-species *B. urinator howensis*. The NORFANZ Cruise specimens (41 including 18 males) have shown that the erection of a species is justified. *B. howensis* is closely related to *B. urinator* Burkenroad, 1936, the principal taxonomic differences being in the lack of a well-defined carina and postero-median spine on abdominal somite 4. Also, the dorsomedian lobule of the petasma, which bears the cincinuli, is barely one third of the total length of the petasma, whereas in *B. urinator* it is about half the length. A further difference may be in the preferred habitat depth, *B. urinator* so far being collected from depths ranging from 2560-4180m (mean 3558m) compared with 1287-1975m (mean 1483m) for *B. howensis*. While only 13 specimens of *B. urinator* have been collected so far, they have been from a wide range of locations in the Indo-West Pacific: southern Indian Ocean, off the approaches to Torres Strait, northwest Pacific and off Kauai Island, Hawaii (Kikuchi & Nemoto, 1991). *Benthesicymus howensis* has so far been collected only from the Lord Howe Rise (type locality) and adjacent West Norfolk Ridge.

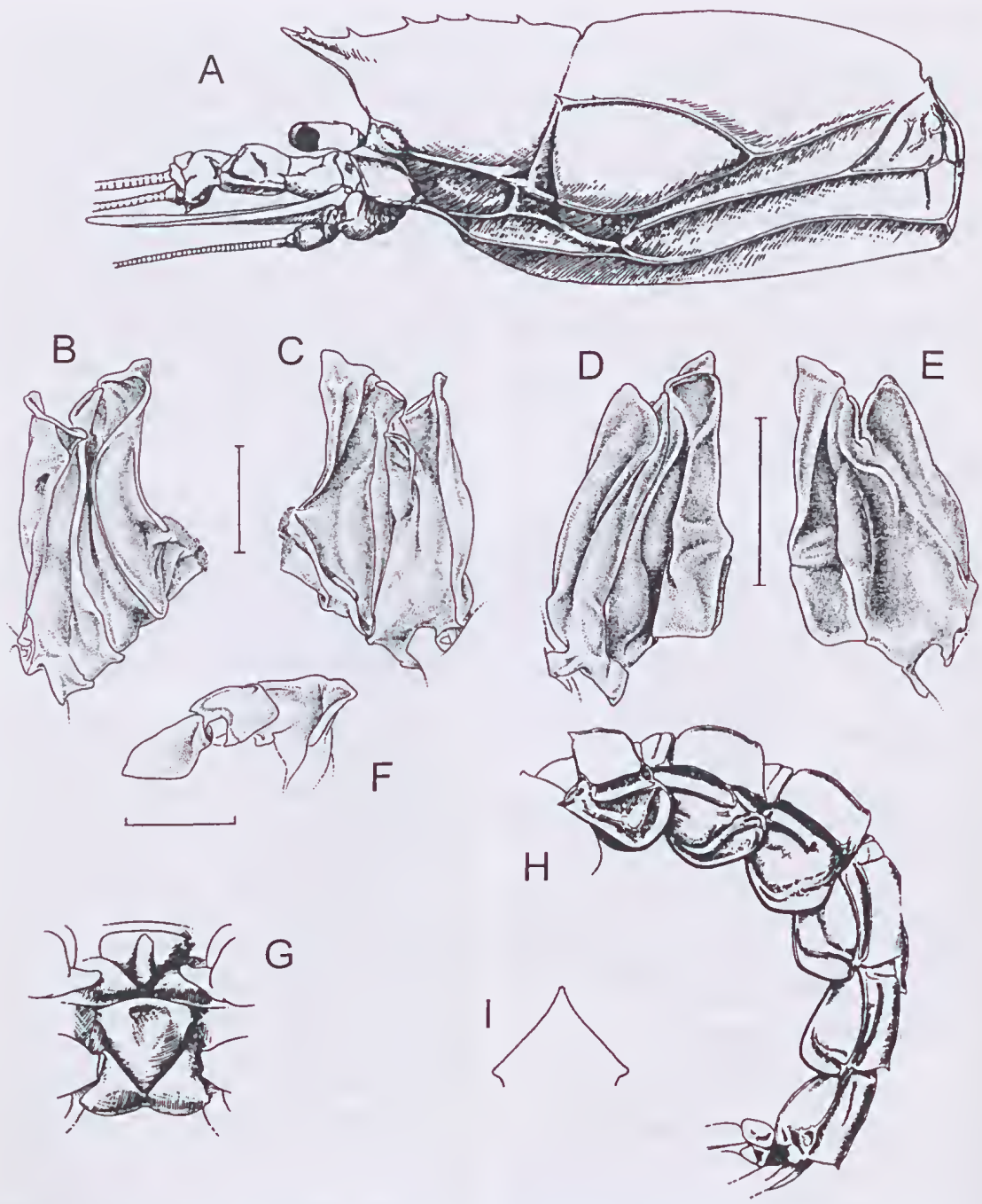


FIG. 2. *Gordonella kensleyi* Crosnier, 1988. ♀ holotype, 53.5 mm, A, anterior half of body, G, thelyeum, H, abdomen, I, transverse section of dorsal part of somite 3; B, C, F NORFANZ Cruise, Stn. 103, 33°46'S, 167°29'E, 1430-1460 m, ♂, 53 mm, left half petasma, B, anterior face, C, posterior face, F, upper part viewed from above; D, E, Cruise Halipro, Stn.Bt 82, 23°56'S, 168°28'E, 1846-1869 m, ♂ 47.6 mm, left half of petasma, D, anterior face, E, posterior face. Scale = 5mm. A, G, H, I are reproduced from Crosnier, 1988, with the authorization of © Publications Scientifie du Muséum national d'Histoire naturelle, Paris. B–E are original, exeeuted by J. G. Dejouannet of the Muséum national d'Histoire naturelle, Paris.

### **Gennadas gilchristi** Calman, 1925

*Gennadas gilchristi* Calman, 1925: 6, pl.1, figs 3, 4; Burkenroad, 1936: 36, fig. 58; Barnard, 1950: 633, 118g, h; Kensley, 1968: 301; 1971: 280, fig. 6; Griffith & Brandt, 1983: 179; Kensley et al., 1987: 277; Iwasaki & Nemoto, 1987; Dall, 2001: 431, fig. 16.

MATERIAL. (All under 9mm); Station 82, ♂; Station 89, ♂; Station 120 ♂; Station 129, ♂; Station 140, ♂; Station 142, ♂, ♀; Station 151, 3 ♀; Station 158, 2 ♂; Station 163, 2 ♀; Station 164, 2♂, ♀; Station 166, ♂, 2 ♀

REMARKS. This is a mesopelagic species with a preferred depth range of 200-700m; it is the commonest *Gennadas* species in southeastern and southern Australian seas. Recorded range: off Cape Peninsula and west coast of S. Africa, Argulhas Basin, S. Indian Ocean, S. and SE Australia (33°-45°S), Norfolk Ridge.

### **Gennadas kempi** Stebbing, 1914

*Gennadas kempi* Stebbing, 1914: 283, pl. 27; Calman, 1925:4; Burkenroad, 1936: 68, figs 52, 54; Barnard, 1950: 630, figs 118a-d; Kensley, 1971: 285, fig. 8; Kensley, et al., 1987: 278; Iwasaki & Nemoto: 1987, 38; Dall, 2001: 432, fig. 18.

MATERIAL. Station 163, ♀.

REMARKS. The sole NORFANZ record is almost at the known northern limit (32°S) of this species. It is unique in that it is an Antarctic species, recorded down to 62°27'S , between 115° – 150°E (Iwasaki & Nemoto, 1987).

Known range: SE Indian Ocean, S and SE Australia, Antarctic Ocean, New Caledonia basin, SE Atlantic Ocean, 0-3400m; probably a mesopelagic species.

## Family SOLENOCERIDAE Wood-Mason 1891

*Solenocerina* Wood-Mason, 1891: 275.
*Solenocerinae* Burkenroad, 1934b: 63; Ramadan, 1938: 56; Crosnier, 1978: 14, 96, 1985: 31; 1988: 563; 1989, 379.
*Solenoceridae* Pérez Farfante, 1978: 2, 1988: iv, 26; Grey et al. 1983: 14; De Freitas, 1985: 28; Pérez Farfante & Kensley, 1997: 157; Dall, 1999: 555.

For diagnosis and keys see Pérez Farfante & Kensley, 1997 and Dall, 1999.

### **Gordonella kensleyi** Crosnier, 1988 (Fig. 2)

*Gordonella kensleyi* Crosnier, 1988:597, figs 2e, 12b, 15h,i, 16g.
*Haliporus villosus* Kensley, 1968.

MATERIAL: Station 47, 2♂ 46, 50mm, ♀ 65mm (damaged); Station 71, 2♂ 44, 51mm, 3♀ 55-69mm; Station 73, 2♂ 22, 42mm, ♀ 22mm; Station 101, 3♀ 58, 68, 68mm (damaged); Station 103, 2♂ 49, 53mm, 2♀ 47, 59mm; Station 168, one, badly damaged.

DIAGNOSIS: Integument glabrous, soft, flexible; cephalothorax bulbous with relatively slender abdomen and long pleopods. Rostrum acute, slender, reaching about middle of second segment of antennular pedunele, with two or three dorsal teeth; four or five postrostral teeth, with indications of additional posterior tooth.

Carapace with post-orbital, antennal, pterygostomian, hepatic and supra-hepatic spines; post-orbital, antennal, hepatic, branchiostegal and accessory carinae present (Fig. 2A). Abdomen with prominent lateral carinae; dorso-median spines on third, fourth and fifth somites; dorsum of third somite acutely pointed (Fig. 2H, I). Petasma (Fig. 2B, F) has cincinuli for about lower one third of inner margin; extremity of ventro-median lobule slightly thickened and bluntly pointed; dorso-lateral lobule poorly defined and ventro-lateral lobule slightly hollowed with blunt angular tip. Thelycum (Fig. 2G) with triangular plate on fifth sternum, apex directed posteriorly, anterior edge slightly convex; fourth sternal plate of similar shape, but smaller with longitudinal, median swelling.

REMARKS. At present there are only three species within this genus: *G. villosa*, *G. paravillosa* and *G. kensleyi*. The first is known only from the type, which is in very poor condition. *G. paravillosa* has been collected off northeast Australia and Indonesia, whereas *G. kensleyi* has been found off South Africa and New Caledonia, as well as the NORFANZ locations of Lord Howe Rise and West Norfolk Ridge. This the first time that males of this species have been collected. The depth range for NORFANZ material was 1132-1934m compared with recorded depths of 1510-2798m.

### **Hadropenaeus lucasii** (Bate, 1881)

*Solenocera lucasii* Bate, 1881: 185.
*Philonicus lucasii* Bate, 1888: 62.
*Pleoticus lucasii* Bate, 1888: 227, pl. 42, fig. 4.
*Haliporus Lucasi* Bouvier, 1908: 80.
*Haliporus lucasii* de Man, 1911: 7, 41 43.
*Hymenopenaeus lucasii*, Burkenroad, 1936; Anderson & Lindner, 1945: 289; Kubo, 1949: 213, figs 8B, 20Q, 27K-N, 66O,P, 72C,I, 80H, 91, 92A-C.
*Hymenopenaeus lucasi* Crosnier & Forest, 1973: 260; Crosnier, 1978: 115, figs 37f-h, 39c, 43a, 44.
*Hadropenaeus lucasi* Crosnier, 1989: 44; 1994b: 369; Kensley et al., 1987: 17 .
*Hadropeneus lucasii* Pérez Farfante, 1977: Hayashi, 1984b: 445, fig. 78; Dall, 1999: 560, fig. 5.

MATERIAL. Station 106, ♂ 13mm, 2♀ 16,18mm; Station 107, 8♀ 15-21.5mm; Station 108, ♂ 20mm; Station 132, 2♂ 10, 13.5mm

REMARKS. All specimens were collected on the West Norfolk Ridge at depths of 121-698m, extending the known depth range; distribution is from Mozambique to Indonesia, NW and E Australia, Wallis Islands, Japan and Hawaii.

### **Haliporoides sibogae** (de Man, 1907)

*Haliporus sibogae* de Man, 1907: 38; 1911: 7, 38; 1913: pl. 3, fig. 10a-b, pl. 4, fig. 10c-q.
*Haliporoides sibogae* Pérez Farfante, 1977: 290; Crosnier, 1984; 1989: 44; 1994; Grey et al., 1983: 15: Hayashi, 1984b: 445; Yu & Chan, 1986; Dall, 1999: 562, fig. 6B.
*Haliporoides sibogae australiensis* Kensley et al., 1987:562.
*Hymenopenaeus sibogae* Crosnier, 1978: 104, figs36a, 38d; 1985: 23.
*Parahaliporus sibogae* Kubo, 1949: 208, figs 1O, 8C, 9A, 14D, 231J, 36A-D, 44E, 66Q,R, 68O, 72E,K, 81D, 90.

MATERIAL. Station 6, ♂ 30mm; Station 64, 2♂ 34, 35mm; 3♀ 35-45mm; Station 81, 3♂ 21, 22, 36mm; 2 ♀(damaged); Station 82, 2 juveniles; Station 83, 2♂ 33, 35mm; ♀ 30mm; Station 89, 8♂ 22-33mm; 3♀ 43-47mm; Station 108, 2♀ 43-47mm; Station 125, ♀ 38mm.

REMARKS: Nearly all were collected on the Norfolk Rise and West Norfolk Ridge at depths between 542-780m. Range: Madagascar to Indonesia, NW and E Australia, South China Sea, Japan and New Zealand at depths between 100-900m. Has been fished commercially off the New South Wales coast.

### **Hymenopenaeus methalli** Crosnier & Dall, 2004

*Hymenopenaeus methalli* Crosnier & Dall, 2004: 17.

MATERIAL. Station 43, ♂ 17mm; 2♀ 16-21mm; 9 juveniles, damaged; Station 80, 2♀ 20mm; Station 102, 3♂ 12, 20, 20mm; Station 108, 2♂ 20mm; Station 147, 2♀ 20, 25mm.

REMARKS. Station at 26°25.94'S was at the northern limit of the Cruise; the remainder were either on the Lord Howe Rise or West Norfolk Ridge, depth 750-1478m., but the sole record at 1478m is exceptional, with 930m the maximum recorded elsewhere. The type locality is NW of New Caledonia, 19°42.40'S, 158°50.80'E. and it has been collected around New Caledonia, Vanuatau, Chesterfield and Tonga Islands, at 650-930m.

### **Hymenopenaeus neptunus** (Bate, 1881)

*Haliporus neptunus* Bate, 1881, 1888; de Man, 1911.
*Hymenopenaeus neptunus* Crosnier & Forest, 1973: 128; Crosnier, 1984: 24; 1989: 49, 51; 1994a: 353: 1994b: 370; Dall, 1999: 567, fig.8C.

MATERIAL. Station 73, ♂ 17mm; ♀(no carapace, similar size to male); Station 101, ♀ 16mm; Station 114, 2♂ 20, 21mm; 2♀ 21, 25mm.

REMARKS. The above stations were either on the southern part of the Lord Howe Rise or the West Norfolk Ridge at depths from 1132m to 1470m. This species has been collected from the Indian Ocean to Indonesia, the Philippines, NE Australia, Wallis Islands, depth range 700-1500m, most below 1000m.

### **Hymenopenaeus obliquirostris** (Bate, 1881)

*Haliporus obliquirostris* Bate, 1881: 186; 1888: 286, pl.41, fig.2.
*Hymenopenaeus obliquirostris* Crosnier & Forest, 1973: 264, fig.87e; Crosnier 1989: 49, figs 2c, 4a,b; Pérez Farfante & Kensley, 1997: 173; Lee *et al.*, 2001: 58, figs 2G-K, 3K,L, pl. 1D; Crosnier & Dall, 2004: 3, figs 3-5.

MATERIAL. Station 73, 4♂ 18-21mm; 2♀ 20, 24mm; Station 114, 2♂ 22, 23mm; 3♀ 22, 24, 24mm; Station 121, 3♀ 22, 25, 25mm; Station 123, ♂ 21mm; 2♀ 21, 27mm; Station 142, ♀ 25mm; Station 146, 2♂ 18, 21mm; 2♀ 18-31mm; Station 160, ♂ 19mm.

REMARKS. This species was restricted to the southern part of the Lord Howe Rise and the West Norfolk Ridge, at depths between 969 and 1345m. Until recently the only record of this species was off the Kermadec Islands by the HMS Challenger (Bate, 1881). It was recorded around Taiwan by Lee *et al.* (2001) and in the waters around New Caledonia, as well as the present locality, by Crosnier & Dall (2004). The depth range is 632-1345m.

### **Solenocera comata** Stebbing, 1915

*Solenocera comatum* Stebbing, 1915: 67, pls 13,14; Barnard, 1950: 617, figs 113k, 114; Kensley, 1972: 18, fig. 7c-e; 1974:70.
*Solenocera comatus* Burkenroad, 1934: 71; 1939: 6; Anderson & Lindner, 1945: 287.
*Solenocera brevipes* Kubo, 1949: 246, figs 1S, 8X, 20N, 27F-H, 45D, 66I,J, 72Q,W, 80A, 98II-J, 99, 100.
*Solenocera comata* Crosnier, 1978: 139, figs 48b, 49b, 50d, 51b-e, 52b; 1984:869; 1985: 869; 1994:355; Hayashi, 1984a: 358; Dall, 1999: 577, fig. 16.

MATERIAL. Station 20, 6 juveniles; Station 106, ♂ 14mm, ♀ 15mm.

REMARKS. The absence of *Solenocera* species from most of the collections on this cruise may have been due to two factors: first, most of the trawls were at depths greater than 700m, whereas most *Solenocera* species recorded in the southwest Pacific prefer depths up to 500m; second, they are inhabitants of soft, silty bottoms, which are lacking in the area covered by the Cruise. *S. comata* was collected on the Norfolk Ridge at depths of 126–227m. The known range is the western Indian Ocean, Indonesia, Timor Sea, Philippines, Japan, at 90-460m.

## Family SICYONIIDAE Ortmann, 1898

*Sicyoninae* Ortmann, 1898: 1121; Balss, 1957: 1520.
*Eusicyaninae* Burkenroad, 1934: 116.
*Sicyonidae* Grey et al., 1983: 13, 31.
*Sicyoniidae* Pérez Farfante & Kensley, 1997: 152, Crosnier, 2003: 201.

### Sicyonia inflexa (Kubo, 1949)

*Eusicyonia inflexa* Kubo, 1949: 458, figs. 8O, 48D, 77C,I, 79G, 159, 160A-F.
*Sicyonia inflexa* Starobogatov 1972: 410, pl.11, fig.148b-e; Miyake, 1982: 173, Hayashi, 1985a: 142 ; 1985b: 196, figs 88e, 89e, 91d; 1986: 81, fig. 40; 1992: 151, figs 83e, 84e, 86d; Crosnier 2003: 267.
*Sicyonnia inflexa* Crosnier, 1985a: 46.
*Eusyconia longicauda* Stebbing 1914; Barnard, 1950.
*Sicyonia longicauda* Kensley, 1972:24; 1977:15; 1981,20; de Freitas 1984a:29.

MATERIAL. Station 6, ♀ 10mm; Station 55, ♀ (newly moulted); Station 82, ♂, 2♀; Station 94, ♀ damaged; Station 107, 3♀; Station 126, ♀; Station 150, ♀; Station 154, 5♂, 31 ♀.

REMARKS. Collected on the Norfolk Ridge, the Lord Howe Rise and the West Norfolk Ridge, 292-1150m. Extensively collected from South Africa, Mozambique, Madagascar, Indonesia, N.W. Australia, around New Caledonia, Chesterfield Islands, Tonga, Fiji, Philippines, Taiwan and the South China Sea and Japan, 260-936m.

### Sicyonia truncata (Kubo, 1949)

*Eusicyonia truncata* Kubo, 1949.
*Sicyonia truncata* Starobogatov, 1972: 412; Kensley, 1972: 24; 1981: 20; de Freitas 1984a: 29; 1984b: 3; Hayashi 1985a: 29; 1985e:261; 1992: 152, 162; Burukovsky, 1991: 36; 1992: 495; Takeda & Hanamura, 1994: 11; Crosnier 2003: 238.
*Sicyonia laevis* Rathbun, 1906.
*Sicyonia longicauda* Rathbun, 1906 (in part).

MATERIAL. Station 20, 10 juveniles, 4 – 8mm.

REMARKS. Near Norfolk Island, 322-327m. Recorded from South Africa, Madagascar, Indonesia, N.W. Australia, New Caledonia, Chesterfield Islands, Vanuatu; Fiji, Tonga, Hawaii, Japan, 110-510m depth.

## Family PENAEIDAE Rafinesque-Schmaltz, 1815

*Penedia* Rafinesque-Schmaltz, 1815
*Penaeidae* Dana, 1852a, b; Boas, 1880; Bate 1881, 1888; Ortmann, 1898; Alcock, 1901; Bouvier, 1908; de Man, 1911; Barnard, 1950; Balss, 1957; Pérez Farfante, 1978; Williams, 1984; de Freitas, 1987; Pérez Farfante, 1988; Dall et al., 1990, Pérez Farfante & Kensley, 1997.
*Penaeinae* Ortmann, 1898; Bouvier, 1908; Burkenroad, 1934b; Balss, 1957.
*Parapenaeinae* Ortmann, 1898.
*Funchaliae* Bouvier, 1908; Balss, 1957.
*Haliporae* Bouvier, 1908; Balss, 1957.
*Funchaliinae* Burukovsky & Romensky, 1991.

REMARKS. The Penaeidae is the best known and most numerous of the five families of the Penaeoidea, but two factors may have contributed to the paucity of species of this family on the NORFANZ Cruise: 1) the majority of penaeids inhabit coastal waters less than about 200m depth and most of the NORFANZ collections were made in depths greater than this; 2) seamounts and ridges lack the extensive soft sands and muds characteristic of inshore areas, which are the preferred benthic environment of the most abundant penaeids.

### Funchalia villosa (Bouvier, 1905)

*Hemipenaeopsis villosa* Bouvier, 1905 (part).
*Grimaldi richardi* Bouvier, 1905 (part).
*Funchalia woodwardi* Bouvier, 1908 (part); Lens & Strunck, 1914.
*Funchalia vanhaffeni* Lenz & Strunck, 1914:303.
*?Funchalia* Gurney, 1924.
*Funchalia villosa* Burkenroad, 1936:129; Dall, 1957:163; Crosnier & Forest, 1973:19; Grippa, 1976:80; Kensley, 1977:17; Griffiths & Brandt, 1983:177; Crosnier, 1985:869; Kensley et al., 1987:281; Burukovsky & Romensky, 1991:31.

MATERIAL. Station 71, 2♂ 15, 16mm; ♀ 18mm.

REMARKS. This is a pelagic species (Kensley et.al., 1987) but was collected in a "rateatcher" trawl at 1920-1934m, so presumably was caught when the trawl was being recovered. *Funchalia villosa* has a world-wide, though scattered, distribution. Dall (1957) reported that the Lord Howe Island collection was at that time the first authentic record for the Southern Hemisphere, but Griffiths & Brandt (1983) found that it was commonly associated with warm water eddies in the surface waters down to about 200m.

### Metapenaeopsis velutina (Dana, 1852)

*Penaeus velutinus* Dana, 1852: 604; 1885:pl. 11, fig. 4; Bate, 1881: 175 (part).
*Metapenaeus velutinus* Rathbun, 1906:903.
*Metapenacapsis velutina* Starobogatov, 1972: 406, 409; Burukovsky, 1974: 36(key); 1983: 49; Crosnier, 1991: 247.
*Metapenaeopsis insana* Racek & Dall, 1965:41; Starobogatov, 1972: 406, 408; Burukovsky, 1983: 50.
*Metapenaeopsis caliper* Liu & Zhong, 1988: 238, 269.

MATERIAL. Station 59, 20 juveniles, 8-11mm; Station 61, ♂ 12mm, ♀17mm, plus a large number of juveniles; Station 67, ♂ 8mm, 2♀ 9, 10mm.

REMARKS. All the *M. velutina* were collected in the vicinity of Middleton Reef and Lord Howe Island. Station 59 was recorded as being made with an ORH trawl at 1600m, whereas Stations

TABLE 1. List of Stations where Penaeoidea were Collected. ***Region**: SNR = South Norfolk Ridge; NNR = North Norfolk Ridge; LHP = Lord Howe Plateau; WNR = West Norfolk Ridge. ****Gear code**: 10= ORH trawl. A deep water rough bottom wing trawl used in the Orange Roughy fishery with proven record for seamount fishing; 60mm cod-end option. 11= Nicknamed "Rateateher". A 40mm cod-end wing trawl designed for close bottom fishing for juvenile Orange Roughy on flat soft bottom. 13= Beam trawl. French design with previous success for sampling invertebrate epifauna on similar voyages. 20= NIWA sled. Used successfully for sampling seamounts on previous French cruises. 21= Sherman epibenthic sled, 1.9 m x 2.2 m x 0.8 m high, with 25 mm cod-end mesh. 53= Midwater

| Station No. | *Region | Time | Latitude | Longitude | Depth range(m) | **Gear code |
|---|---|---|---|---|---|---|
| 2 | SNR | 1615 | 34 09.37 | 171 27.79 | 544-584 | 10 |
| 3 | " | 1937 | 34 03.21 | 171 08.1 | 1051-1320 | 10 |
| 6 | " | 0206 | 34 09.14 | 171 27.95 | 542-554 | 21 |
| 8 | " | 0622 | 34 09.75 | 171 27.33 | 558-573 | 21 |
| 16 | " | 0959 | 29 59.62 | 167 38.73 | 1245-1285 | 10 |
| 20 | " | 1926 | 29 41.84 | 168 02.62 | 322-337 | 13 |
| 27 | " | 1907 | 28 54.47 | 167 41.04 | 110-441 | 10 |
| 28 | " | 2121 | 28 51.94 | 167 40.59 | 718-859 | 10 |
| 33 | NNR | 1853 | 28 29.37 | 167 47.15 | 1056-1116 | 10 |
| 43 | " | 1031 | 26 25.94 | 167 10.87 | 750-774 | 13 |
| 44 | " | 1250 | 26 23.53 | 167 01.21 | 1019-1030 | 10 |
| 47 | " | 0227 | 28 29.88 | 161 15.56 | 1530-1530 | 11 |
| 55 | " | 1237 | 29 13.12 | 159 00.45 | 292-330 | 20 |
| 59 | " | 1922 | 29 14.97 | 159 02.72 | 1600-1600 | 10 |
| 61 | " | 2133 | 31 49.11 | 159 20.74 | 86-89 | 21 |
| 63 | " | 0307 | 31 42.53 | 159 07.93 | 798-880 | 10 |
| 64 | " | 0518 | 31 40.55 | 159 09.43 | 587-700 | 10 |
| 66 | " | 1054 | 31 45.73 | 159 20.93 | 565-960 | 21 |
| 67 | " | 1316 | 35 35.83 | 169 33.43 | 72-82 | 21 |
| 71 | " | 0030 | 32 03.98 | 159 52.80 | 1920-1934 | 11 |
| 72 | LHP | 0740 | 32 11.59 | 160 51.66 | 1342-1361 | 11 |
| 73 | " | 1434 | 32 25.94 | 161 47.62 | 1132-1197 | 11 |
| 74 | " | 1906 | 32 26.08 | 161 45.36 | 1171-1259 | 10 |
| 77 | " | 0020 | 32 26.70 | 161 46.95 | 1130-1147 | 13 |
| 78 | " | 0455 | 32 39.33 | 162 33.11 | 864-870 | 13 |
| 80 | " | 0954 | 32 42.50 | 162 33.86 | 850-872 | 11 |
| 81 | " | 1916 | 34 01.95 | 162 35.96 | 780-818 | 11 |
| 82 | " | 0106 | 34 12.44 | 162 39.50 | 758-760 | 13 |
| 83 | " | 0320 | 34 11.83 | 162 37.10 | 761-765 | 10 |
| 86 | " | 0833 | 34 11.06 | 162 39.19 | 430-740 | 21 |
| 89 | " | 1349 | 34 12.18 | 162 41.18 | 748-772 | 11 |
| 90 | " | 1951 | 34 12.17 | 163 21.36 | 1090-1117 | 11 |
| 91 | " | 2217 | 34 12.41 | 163 17.20 | 1076-1083 | 13 |
| 92 | " | 0038 | 34 12.70 | 163 21.59 | 1080-1120 | 10 |
| 93 | WNR | 1854 | 33 49.47 | 167 03.45 | 804-944 | 10 |
| 94 | " | 2124 | 33 49.50 | 166 58.80 | 950-987 | 13 |
| 95 | " | 2326 | 33 49.24 | 167 03.35 | 805-938 | 11 |
| 96 | " | 0433 | 33 37.10 | 166 55.60 | 1017-1042 | 11 |
| 101 | " | 1922 | 33 45.20 | 167 28.30 | 1410-1470 | 10 |
| 102 | " | 2220 | 33 42.45 | 167 27.03 | 1451-1478 | 13 |
| 103 | " | 0055 | 33 46.55 | 167 29.28 | 1431-1460 | 11 |

TABLE 1. *(continued).*

| Station No. | *Region | Time | Latitude | Longitude | Depth range(m) | **Gear code |
|---|---|---|---|---|---|---|
| 106 | " | 1100 | 32 37.58 | 167 35.17 | 121-126 | 13 |
| 107 | " | 1405 | 32 36.49 | 167 43.98 | 699-707 | 13 |
| 108 | " | 1547 | 32 35.67 | 167 44.12 | 698-724 | 11 |
| 114 | " | 0641 | 32 35.22 | 167 47.66 | 1021-1052 | 11 |
| 119 | " | 1501 | 32 32.65 | 167 47.05 | 957-977 | 10 |
| 120 | " | 1747 | 32 36.57 | 167 50.33 | 1303-1313 | 10 |
| 121 | " | 2132 | 32 36.39 | 167 50.59 | 1331-1345 | 13 |
| 123 | " | 0249 | 32 36.23 | 167 47.09 | 926-969 | 11 |
| 125 | SNR | 1832 | 33 23.60 | 170 09.53 | 605-622 | 21 |
| 126 | " | 1931 | 33 23.41 | 171 11.58 | 469-526 | 21 |
| 128 | " | 2314 | 33 23.57 | 170 09.95 | 627-662 | 10 |
| 129 | " | 0450 | 33 29.24 | 170 00.71 | 1158-1230 | 10 |
| 132 | " | 1057 | 33 22.61 | 170 12.70 | 514-540 | 21 |
| 140 | WNR | 1403 | 34 19.14 | 168 24.63 | 831-846 | 10 |
| 141 | " | 1611 | 34 17.09 | 168 21.50 | 785-800 | 13 |
| 142 | " | 1903 | 34 16.49 | 168 24.08 | 1246-1249 | 10 |
| 145 | " | 2346 | 34 17.84 | 168 25.82 | 1251-1268 | 21 |
| 146 | " | 0306 | 34 14.43 | 168 21.18 | 1195-1202 | 11 |
| 147 | " | 0523 | 34 18.14 | 168 23.18 | 809-857 | 11 |
| 150 | " | 1346 | 34 34.99 | 168 55.54 | 1000-1150 | 21 |
| 151 | " | 1641 | 34 34.13 | 168 56.48 | 1013-1340 | 10 |
| 154 | " | 2232 | 34 37.20 | 168 57 03 | 521-539 | 13 |
| 155 | " | 0035 | 34 34.81 | 168 57.79 | 813-1000 | 11 |
| 156 | " | 0241 | 34 34.26 | 168 56.53 | 1013-1350 | 11 |
| 158 | " | 1055 | 35 10.27 | 169 29.24 | 867-869 | 13 |
| 159 | " | 1228 | 35 08.12 | 169 28.37 | 868-872 | 11 |
| 160 | " | 1735 | 34 58.85 | 169 29.60 | 1288-1294 | 11 |
| 163 | " | 2353 | 34 59.13 | 169 26.50 | 1278-1287 | 10 |
| 164 | " | 0409 | 35 15.70 | 169 38.25 | 771-772 | 10 |
| 166 | " | 0734 | 35 17.17 | 169 33.63 | 815-867 | 10 |
| 167 | " | 1200 | 35 35.83 | 169 33.43 | 1760-1789 | 11 |
| 168 | " | 1614 | 35 56.46 | 170 01.01 | 0-1975 | 53 |

61 and 67 were made with a Sherman dredge at 72-89m. The greatest depth recorded in the literature is 320m, so the 1600m for Station 57 is questionabable. *M. velutina* has been recorded from the Seychelles, NW. and E. Australia, South China Sea, Philippines, New Caledonia, Hawaii, 55-320m.

## SIGNIFICANCE OF THE NORFANZ PENAEOIDEA

The area of the NORFANZ Cruise was between 159° E and 172° E, immediately to the south of the New Caledonia Region. The waters around this island and further east, south of the equator, as far as French Polynesia have been thoroughly investigated by the Centre IRD in New Caledonia during the last 25 years. Over 95 species of Penaeoidae have been identified in a region previously thought to be very limited in species numbers (A. Crosnier, pers. com.). The NORFANZ collection might therefore have been expected to be essentially similar to that of the New Caledonia Region but two factors would have modified the species composition: 1) Depth. Most NORFANZ trawls that collected penaeoids were made in depths greater than 400 m (Table 1). The Penaeidae, Solenoceridae and Sicyoniidae usually inhabit waters less than about 400m deep – only 5 NORFANZ stations out of 73 that collected penaeoids were in this category. Aristeidae and Benthesicymidae generally inhabit deeper waters i.e. below 400m

and so depth is not a major limiting factor in species diversity of these families. 2) Latitude. The Cruise was in subtropical waters (approx. 26°–36°S). The greatest diversity of penaeoid species is within the tropics (Dall et al., 1991). This factor would eliminate homeothermous tropical species but include sub-tropical species e.g. in the NORFANZ collection, *Austropenaeus nitidus*, range 26°– 40° S, and *Gennadas kempi*, range 32° – 62° S, (Dall, 2001).

Three species in the NORFANZ collection are cosmopolitan in their distribution (*Aristaeomorpha foliacea, Aristaeopsis edwardsiana* and the pelagic *Funchalia villosa*). Twelve extend through the Indo-West Pacific (*Aristeus mabahissae, A. virilis, Hepomadus tener, Benthesicymus investigatoris, Gennadas gilchristi, Hadropenaeus lucasii, Haliporoides sibogae, Hymenopenaeus neptunus, Solenocera comata, Metapenaeopsis velutina, Sicyonia inflexa, S. truncata*). All of these species have been recorded for E. Australia (Crosnier, 1991, 2001; Dall, 1999, 2001) so these records can be regarded as extending their known range into the eastern sub-tropics of the Tasman Sea.

The rare species, *Gordonella kensleyi*, has been recorded in the Mozambique Channel and immediately south of New Caledonia (Crosnier, 1988), so the NORFANZ record extends its range. It will probably be found in eastern Australia and other intermediate locations. Until recently the only record of *Hymenopenaeus obliquirostris* was from the Kermadec Islands by the CHALLENGER in 1881, but it has now been found around Taiwan (Lee et.al., 2001), New Caledonia and the NORFANZ area (Crosnier & Dall, 2004). With such widely separated locations it is likely to be found in intermediate areas. *Hymenopenaeus methalli* is reported from the New Caledonia Region as far as Tonga and in the NORFANZ area, a limited range for a member of this genus.

Overall the NORFANZ collection gives no indication that the area is faunistically isolated for the Penaeoidea, except for *Benthesicymus howensis*, which has not been collected outside the NORFANZ area. All other species collected have a wide distribution at least in the southwest Pacific, most in the Indo-West Pacific. The types of *Benthesicymus howensis* were from the Lord Howe Rise, but specimens were also collected by NORFANZ on the West Norfolk Ridge. Since this ridge extends well into the New Caledonia Region, it is likely that *Benthesicymus howensis* has a wider distribution.

Since the Penaeoidea probably all have planktonic larvae, endemism on seamounts and ridges of the Tasman Sea is unlikely. Many of the adults of the species collected by the NORFANZ are bathypelagic or mesopelagic, but even if an adult population on a seamount was surrounded by depths well beyond their normal range, their planktonic larvae could bridge these in time.

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# FOSSIL FRUIT OF THE GREVILLEEAE (PROTEACEAE) IN THE TERTIARY OF EASTERN AUSTRALIA

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Dettmann, M.E. & Clifford, H.T. 2005 12 31: Fossil fruit of the Grevilleeae (Proteaceae) in the Tertiary of eastern Australia. *Memoirs of the Queensland Museum* **51**(2): 423-438. Brisbane. ISSN 0079-8835.

*Conchotheca rotundata* F.Muell., 1873 a fossil fruit taxon described from mid-Tertiary deep lead sediments at Haddon, Victoria is morphologically and anatomically consistent with fruits of extant *Grevillea* (Tribe Grevilleeae). The fossil taxon, which is redefined on the basis of the type and other specimens, accommodates uniloculate, tardily dehiscent, ellipsoidal fruits with stalk attachment displaced laterally towards the style and a thick, woody pericarp that is radially structured. The fossil fruit evidence taken together with that of fossil leaves and pollen associated with *Grevillea* demonstrate a history of the Tribe to at least the latest Cretaceous (Maastrichtian) in the Australian vegetation. *Conchocaryon smithii* F.Muell., 1879, a fossil fruit from Miocene sediments at Gulgong, New South Wales may also have affinities with Tribe Grevilleae, but the protocol specimen, which is refigured herein, has not been located and is believed lost. For comparative purposes, fruit and seed structure are documented of extant members of Tribe Grevilleae (*Grevillea*, *Hakea*, *Finschia*) and of *Buckinghamia* (sister to Grevilleae on molecular evidence). □ *Proteaceae, Grevillea, Conchotheca, Conchocaryon, fossil fruit, Australia, Tertiary.*

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The Tribe Grevilleae comprises three genera, two of which (*Grevillea* Knight ~363 spp., *Hakea* Schrad. & J.C. Wendl. ~150 spp.) are the most species-rich of the Proteaceae in the Australian flora, plus *Finschia* Warb.with four species centred in New Guinea and adjacent islands (Fig. 1). Whereas *Finschia* are mostly tall trees of rainforests, open woodlands and swamp forests in high rainfall areas, *Hakea* (endemic to Australia) has near pan-Australian distribution and is concentrated in the drier regions, occurring as low trees and shrubs in open woodlands, heathlands, and coastal communities. *Grevillea*, with its distribution centred in Australia (357 spp.), extends to New Caledonia, New Guinea and Sulawesi, includes tall trees and shrubs of closed to open forests and woodlands (mostly in high rainfall or monsoonal regions of northern and eastern areas of its range), and small trees to spreading and prostrate shrubs especially under lower rainfall regimes in southern and Western Australia.

By contrast to the high diversity levels and almost pan-Australian distribution of *Grevillea* and *Hakea* in the present-day vegetation, their past history is virtually unknown from the fossil record. The possible occurrence of the genera in Australia during the Tertiary was first hinted at by Mueller (1873: 41). He noted the 'general appearance' of fossil fruits attributed to *Conchotheca rotundata* F.Muell. to pericarps of three extant *Grevillea* species. Although arguing against assigning the fossils to *Grevillea*, he later (1882: 44) noted that they, like the pericarps of *Grevillea*, are attached to stipes that are laterally displaced with respect to the style. The fossils were recovered from deep lead sediments during gold mining activities in the 1850's-1870's near Haddon, Victoria (Mueller, 1873, 1874a,b), and subsequently reported (Mueller, 1879; Barnard, 1881) to have been recovered from beneath Tertiary basalts at Beaconsfield near Launceston (Tasmania), Clifton (Queensland) and Gulgong (New South Wales). Another fossil fruit taxon, *Conchocaryon smithii* F.Muell. (1879: 39) most likely from the Gulgong locality was described as resembling pericarps of *Grevillea* and *Hakea*. The enclosed seed, which was reported with a 'terminal wing-like appendage', intimated a closer resemblance to *Hakea* than *Grevillea*. The fossil taxon was discriminated from *Hakea* on account of possessing only one seed, and a pericarp with a 'lesser degree' of dehiscence. No further evaluation of the systematic affinities of either *Conchotheca rotundata* or *Conchocaryon smithii* has been undertaken and there is no reference to them in reviews of the macrofossil record of Australian Proteaceae (Carpenter, 1994; Hill et al., 1995).

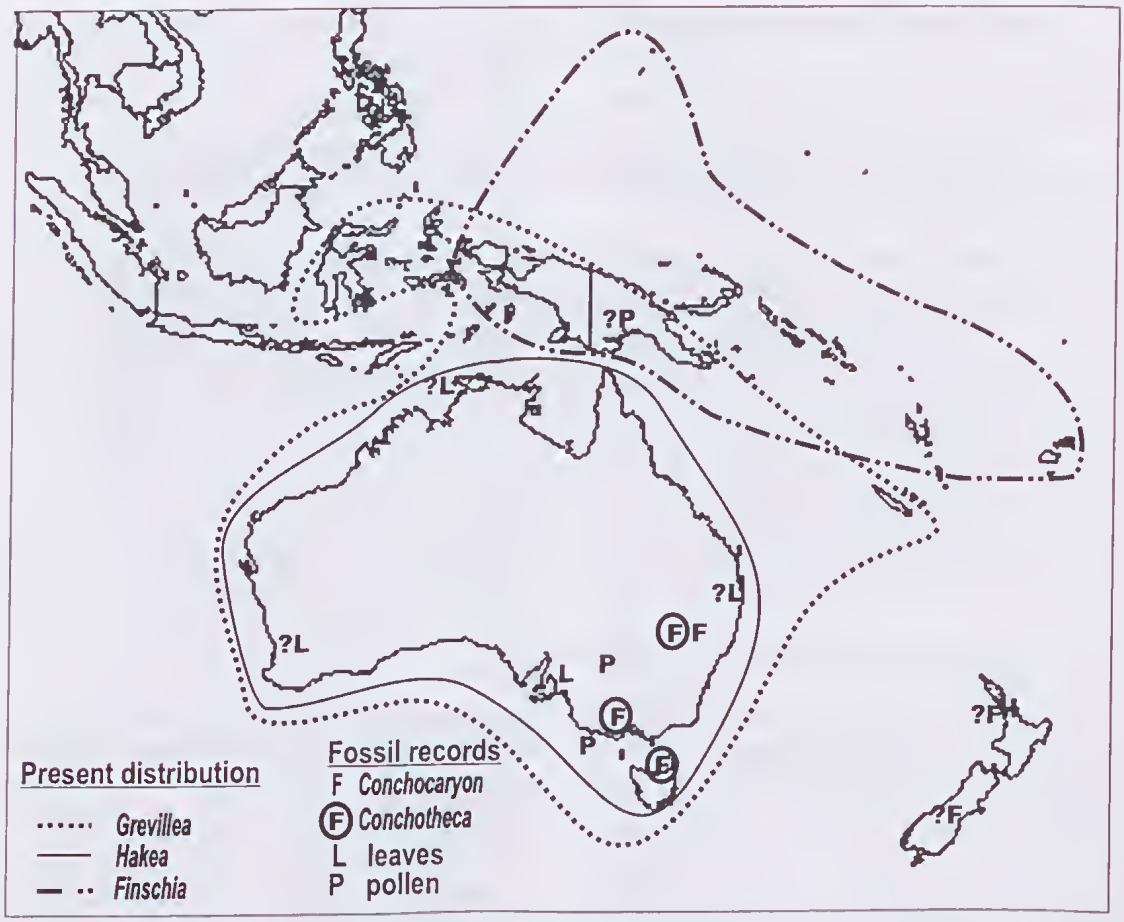



FIG. 1. Map of the southwest Pacific region showing present distribution range of *Grevillea, Hakea,* and *Finschia* and locations from which fossil fruits, leaves, and pollen that conforms with Tribe Grevilleeae have been reported; also indicated are doubtful fossil records of the Tribe.

To elarify the status and affinity of Mueller's taxa, protoeol speeimens were sought from museums in Vietoria and New South Wales. The single speeimen on whieh *Conchotheca rotundata* was based was loeated in the Museum of Vietoria together with several other speeimens subsequently eolleeted. No speeimens of *Conchocaryon smithii* were found; the speeies was defined on the basis of one speeimen, but neither it nor subsequently reported speeimens were loeated. Comparisons have been undertaken of available fossil material with fruits of the three Grevilleeae genera (*Grevillea*, *Hakea*, *Finschia*), and of *Buckinghamia* F.Muell. (Tribe Embothrieae), whieh on moleeular evidenee is the sister group to Grevilleeae (Hoot & Douglas, 1998). Fruits of the extant genera are deseribed and figured and the fossil reeord of Grevilleeae is reviewed.

## MATERIAL

Fossil fruits investigated inelude the protoeol material and other speeimens of *Conchotheca rotundata* F.Muell.,1873 housed in the eolleetions of the Museum of Vietoria (eatalogue numbers prefixed NMVP). The fruits are woody, some retaining well preserved anatomieal charaeters, and others are vitrinised and/or pyritised with few anatomieal features preserved. None retains original seed material, whieh appears to have been lost sinee investigated by Mueller (1873). Speeimens examined are from Smythe's Creek (Reform Co. Shaft, ~47.5m) and Nintingbool (Crueible Co. Shaft ~ 23.2m), near Haddon (37°18'S 146°32'E), SW of Ballarat,

Victoria. These were collected from deep lead sediments that underlie Miocene basalts. An Oligocene or Early-Middle Miocene age of the sediments has been considered most likely (Rozefelds & Christophel, 1996; Dettmann & Clifford, 2001). Specimens were reported from probable Oligocene sediments at Ophir Gold Mine, Beaconsfield, Tasmania (Mueller, 1879), Middle Miocene sediments in Black Lead, Gulgong, New South Wales (Barnard, 1881) and Clifton, Queensland (Mueller, 1879), but these have not been located. No material of *Conchocaryon smithii* has been located; the single specimen described and illustrated by Mueller (1879) probably came from deep lead sediments of Middle Miocene age at Gulgong, New South Wales (Dettmann & Clifford, 2001).

Comparative material investigated (Appendix) includes fruits of several *Grevillea* and *Hakea* species and of *Buckinghamia celsissima* F.Muell. cultivated or from the wild in southeastern Queensland. Developmental stages of fruit maturation were traced for several of these species whose identities were verified by reference to the collections of the Queensland Herbarium. Additionally mature fruit of *Grevillea candicans* C.A. Gardner were obtained from Kings Park, Perth, Western Australia, and of *Finschia chloroxantha* Diels from the Singapore Herbarium.

## METHODS

Fossil and modern fruits were studied using a binocular dissecting microscope. Several of the woody fruits were sectioned in the transverse and longitudinal planes using a jeweller's saw, and the resulting surfaces polished on fine emery paper to reveal details of anatomy. Specimens photographed include the type specimen of *Conchotheca rotundata* illustrated by (Mueller, 1873, 1874b); this specimen is depicted in Figs 2B-G, 4C,D together with reproductions of the original lithographic illustrations (Fig. 2A). Additional anatomical detail was obtained for fruits of *Grevillea heliosperma* R.Br., *Hakea laurina* R.Br., *Finschia chloroxantha*, and *Conchotheca rotundata* from fragments mounted on stubs and gold plated for scanning electron microscope analysis using a Phillips instrument.

Several developmental stages of fruits and seeds were studied in *Grevillea robusta* A.Cunn. ex R.Br., *G. hilliana* Maiden, *Hakea actites* W.R.Barker, and *Buckinghamia celsissima*. Dissected ovaries and hand cut sections of young fruits were cleared in a weak solution of sodium hypochlorite for 1-2 hours, followed by thorough washing in distilled water and mounting in glycerine jelly on glass microscope slides. Anatomical characters of mature seed coats were examined in transmitted light after clearing as designated above.

To provide a basis for the comparison of fossil and living fruits, morphological and anatomical features of fruits of several modern species of *Grevillea, Hakea, Finschia* and *Buckinghamia* are outlined in Appendix.

## SYSTEMATIC PALAEOBOTANY

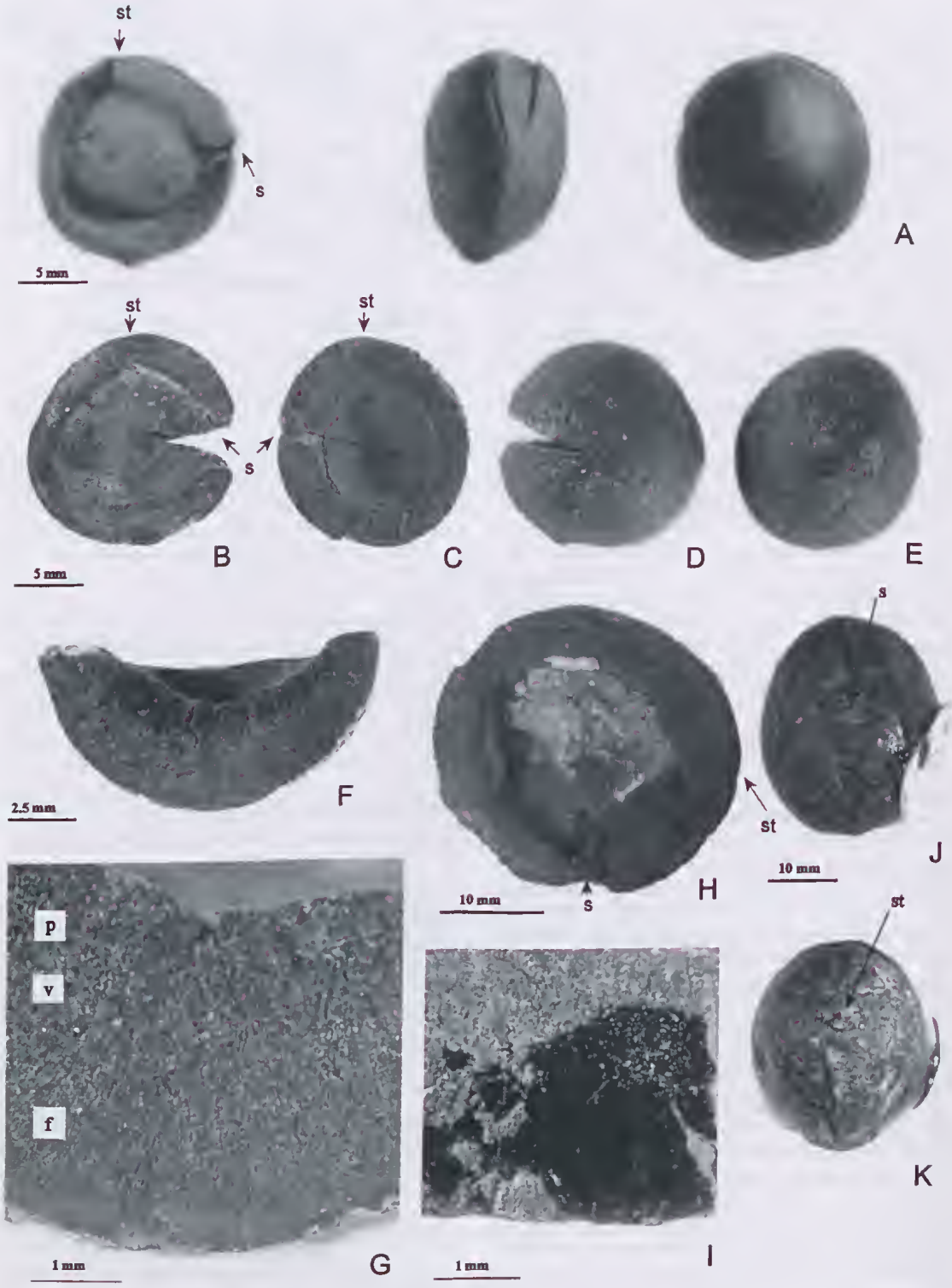
### **Conchotheca** F.Muell., 1873, emend.

1873 *Conchotheca* F.Muell., p.41.

TYPE SPECIES (by monotypy). *Conchotheca rotundata* F.Muell., 1873, emend.

EMENDED DIAGNOSIS. Fruit laterally compressed prolate ellipsoidal or spheroidal, with bilateral symmetry only about the plane that includes stalk, style base, and ventral suture (potential dehiscence line); indehiscent or tardily dehiscent, splitting into 2 equal portions; uniloecular. Stalk base displaced dorsiventrally (laterally towards style), the ventral suture longer than dorsal hinge line. Surface smooth or near-smooth. Fruit wall in transverse section radially structured, the outer pericarp with radially aligned fibres, the middle pericarp with radially aligned fibres associated with predominantly longitudinal vascular bundles, and the inner pericarp predominantly of parenchyma. Seed laterally attached, solitary filling, or almost so, locule. Seed flat, roundish, unwinged.

REMARKS AND COMPARISON. When proposed the genus was monotypic and based on a single specimen (Mueller, 1873: 41, pl. 6, figs 9-11), which is re-figured herein (Figs 2A-G, 4C,D); the seed referred to by Mueller has not been located. Additional specimens were subsequently collected (Mueller, 1882: 44; 1883), but none was illustrated. Mueller (1882) noted further characters of the seed (flat-compressed, almost truncate at one extremity, slightly apiculate at the other; testa membraneous, minutely granular), but none of the specimens we examined possesses seed tissue. Nevertheless, the vascular trace from the ovary wall to the placenta confirms lateral attachment of the seed. A second species, *C. turgida*, referred to the genus by Mueller (1874a: 42, 1874b: 24) was differentiated from *C.*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*rotundata* in being smaller and with a thinner-walled pericarp. Illustrated specimens of *C. turgida* comprise two morphologically distinct forms, each of which differs from *Conchotheca* F.Muell. emend., in that their styles and stalks are in vertical alignment, their ventral sutures and dorsal hinge lines are equal in length, and their seeds are apically attached. Both forms are excluded from *Conchotheca* as emended herein, and will be transferred to a new genus (Dettmann & Clifford, in prep.).

*Conchocaryon* F.Muell., 1879, a monotypic genus based on a single specimen of *C. smithii* F.Muell. 1879, was described as possessing several of the characters displayed by *Conchotheca*, but was segregated on account of its shape being 'unsymmetrical' rather than ellipsoidal. A further distinction noted between the two genera was that the seed of *Conchocaryon* was described as possessing 'a flat terminal appendage' (wing) in contrast to the unwinged seed of *Conchotheca* (Mueller, 1879: 39). The specimen on which *Conchocaryon* was based has not been located in museums in Sydney or Melbourne, and is presumed lost. Detailed comparisons between the two genera were thus precluded.

**Conchotheca rotundata** F.Muell. 1873, emend.
(Figs 2, 3A-D, 4C,D)

MATERIAL. HOLOTYPE (by monotypy): NMVP53971 (2 valves of follicle; vertical axis 14mm; lateral axes, 12.5mm (in plane of dehiscence) x 10mm; pericarp wall 2-3mm thick), Figs 2A-G, 4C,D. OTHER MATERIAL. NMVP53972, NMVP53553, NMVP206494 (Coll. R.A. Lock, Nintingbool, but identified by F.Mueller as *Conchotheca turgida*).

TYPE LOCALITY. Deep leads at Haddon, Nintingbool (Crucible Co. Shaft, ~23.2m), Victoria; ?Early-Middle Miocene.

DESCRIPTION. Fruit prolate ellipsoidal to subspheroidal, bilaterally symmetrical about the plane that includes stalk, stigma, and potential dehiscence line or ventral suture; indehiscent or tardily dehiscent; unilocular, with 1 laterally inserted seed. Stalk attachment displaced dorsiventrally; ventral suture twice length of dorsal hinge line. Stalk base circular, 1-2mm in diameter; style base inconspicuous, represented by faint scar. Fruit with a smooth or near-smooth surface. Pericarp up to 2-3mm thick at midpoint of lateral surfaces, tapering to 1.5-2mm at ventral suture and dorsal hinge line. In section pericarp radially structured, the outer and middle pericarp with radially aligned fibres directed outwards from the predominantly vertically aligned vasculature that demarcates the boundary between the middle and inner pericarp, the latter of which is composed predominantly of parenchyma. Seed flat, roundish, unwinged.

DIMENSIONS. Fruit; length 11.5 (12.8) 14mm; lateral axes, 10 (11.8) 13.5mm (in plane of dehiscence) x 9 (10.6) 13mm (at right angles to dorsal-ventral plane). Seed dimensions unknown.

REMARKS. One valve of the holotype has cracked and split since illustrated (Mueller, 1873, pl. 6, figs 9-11; Mueller, 1874b, pl.6, figs 9-11).

The dorsiventral displacement of the stalk with respect to the style in the fruits was not specified in the original diagnosis, but was hinted at by Mueller's comparison of the fossils with fruits of three species of tropical *Grevillea* (Mueller, 1873: 41). He emphasised (Mueller, 1882: 44) the asymmetry of *Conchotheca rotundata* in lateral views, noting that it 'seems to have its fruit laterally affixed to a stipes (sic)'. Thus, the dorsal hinge line is considerably shorter than the ventral suture (Figs 2A,B,C,H, 4C), a feature of fruits of extant *Grevillea*, and here illustrated for *G. candicans* (Fig. 5H), *G. heliosperma* (Figs 4A, 5A,B), and *G. robusta* (Fig. 5L,M).

Mueller's characterisation of the seed is accepted herein even though no seed material has been observed in the holotype and other specimens studied; it appears that the seed material described by Mueller has been lost or

FIG.2 (facing). *Conchotheca rotundata* F.Muell. A-G, Holotype, NMVP53971, H-K, from Nintingbool (Crucible Co. Shaft, ~23.2 m), Victoria. A, Lateral views showing interior of locule, and external views showing dorso-ventral suture before separation into two valves and lateral surface respectively as illustrated by Mueller (1873, pl. 6, figs 9-11), arrows indicate position of stalk (s) and stigma (st); B,C, interior views of locule, arrows point to stalk (s) and stigma (st); D,E, external views of lateral surfaces; F,G, section of valve cut transverse to ventral suture and dorsal hinge line showing inner pericarp with isodiametric cells (p), and middle and outer pericarp with vasculature (v) and radially aligned fibres (f); H,I, NMVP206494, lateral view of interior of valve showing locule with infilling of sulphur and detail of pericarp wall in longitudinal section respectively; J,K, NMVP53972, basal and apical views showing scars of stalk (s) and stigma (st).

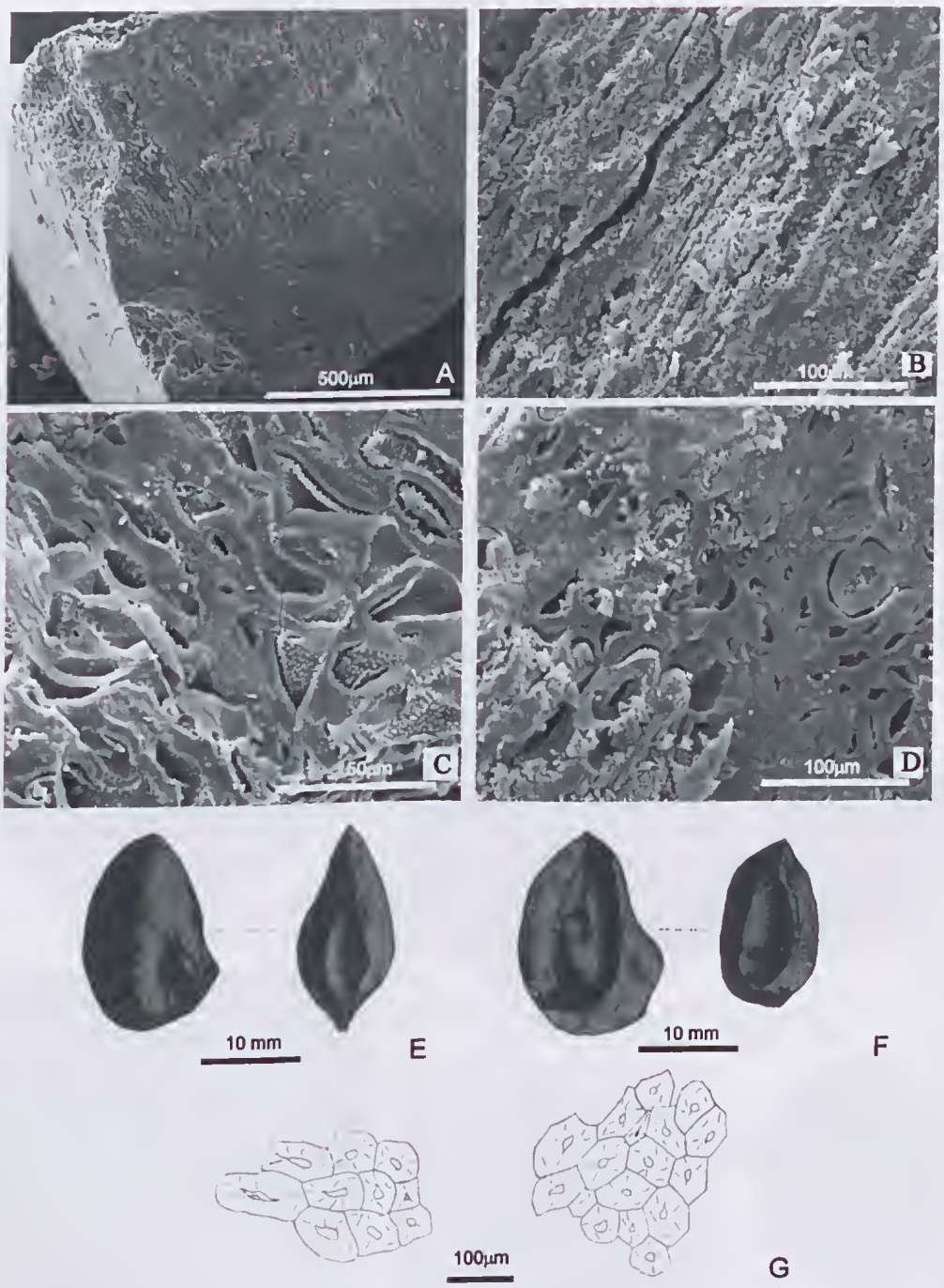



FIG. 3. A-D, *Conchotheca rotundata*, NMVP206494 from Ningtinbool (Crucible Co. Shaft, ~23.2 m), Victoria. A, Portion of pericarp in transverse (large face) and longitudinal (face on left) section; B, radially aligned fibres in middle and outer pericarp; C-D, Fibres in oblique and transverse section surrounding vasculature in mid region of pericarp. E-G, *Conchocaryon smithii*, holotype. E,F, Oblique, basal and lateral views as illustrated by Mueller (1879, pl. 17, figs 4,5); G, detail of pericarp fibres as illustrated by Mueller (1879, pl. 17, fig. 6).

destroyed. Mueller (1873: 41) stated that the fruit possessed one 'flat, roundish' seed, and later remarked (Mueller, 1882: 44) that 'the well-developed seed completely fills the cavity, is flat-compressed, almost truncate at one extremity and slightly apiculate at the other'. He further noted (1882: 44) that 'the testa is membranous, minutely rough from granular elevations, which are mostly arranged in short lines, giving to the outside of the seeds a pretty appearance'.

DISTRIBUTION. (Fig. 1): Haddon (Smythe's Creek, Reform Co. Shaft, ~47.5m; Ningtingbool, Crucible Co. Shaft ~ 23.2m), Victoria (Mueller, 1873, 1874a); Ophir Gold Mine, Beaconsfield, Tasmania (Mueller, 1879b); Black Lead, Gulgong, New South Wales (Barnard, 1881).

AGE RANGE. ?Oligocene-Miocene

AFFINITY. Mueller (1873: 41) considered *C. rotundata* distinct from *Grevillea* in lacking a 'conspicuous stipe' (gynophore), but subsequently acknowledged that '*Conchotheca rotundata* seems to have its fruit laterally affixed to a stipe, as in the case with many Grevilleas' (Mueller, 1882: 44; 1883: 21). In the absence of flowers and leaves he cautioned against placing the species in *Grevillea*.

We confirm that the *C. rotundata* fruit is morphologically consistent with those of *Grevillea*, and shares with them the following characters: asymmetrical except about the plane of potential dehiscence; dorsal hinge line shorter than ventral suture; lateral attachment of seeds; and radially aligned fibres in the middle and outer pericarp. *C. rotundata* is tardily dehiscent in contrast to *Grevillea* fruits, which have readily dehiscent follicles except for fruits of *G. candicans*, which are indehiscent.

In terms of size and shape Mueller (1873) noted resemblance of *C. rotundata* to fruits of several taxa of *Grevillea* referred to the Hilliana and Heliosperma Groups (sensu Makinson, 2000), and especially *Grevillea refracta* R.Br., *G. mimosoides* R.Br., and *G. polystachya* R.Br. (= *G. parallela* Knight). These and other species of the Hilliana and Heliosperma Groups of *Grevillea* have fruits in which the stalk attachment is dorsiventral with respect to the style base, and the thick pericarp wall is composed predominantly of radially aligned fibres in the middle and outer zones external to the vascular bundles (Fig. 5D-F) as described and illustrated by Filla (1926, figs 36-38, 70d). In these respects the fruit wall of *Conchotheca rotundata* is comparable (Figs 2F,G,I, 3A-D), and moreover, as in *Grevillea* fruits, the wall is thickest midway between the ventral suture and dorsal hinge line (Figs 2F, 4D). However, fruits of all extant taxa other than those of *G. candicans* (Fig. 5H, I) are readily dehiscent, although is some species like *G. heliosperma,* (Figs 4A,B, 5A-C) and *G. refracta*, the suture may be barely evident until the latest stages of ripening.

Most *Grevillea* fruits have two laterally attached seeds, but the number may be reduced to one by abortion. In some species the seeds have a broad peripheral wing (Fig. 5G,N), but in the majority of species, the seeds are unwinged (Fig. 5K). Although the unwinged seeds lack a broad peripheral papery wing, they have a circumferential structure such as a 'rib' or 'ruff' that may be a wing-homologue. One-seededness is far more common amongst species with unwinged seeds than in species with winged seeds. *C. rotundata* was described (Mueller, 1873) as having one, unwinged seed, but seed material is absent from specimens examined, and thus unambiguous verification of a *Grevillea* affinity for *C. rotundata* is precluded.

Tardily dehiscent, usually one-seeded fruits that are borne on lateral stipes also occur in *Finschia* (Sleumer, 1955) and *Hakea* (Barker et al., 1999). *Finschia* is distinct in possessing a corky pericarp comprising an exocarp of corky cells and a thick mesocarp of large stone cell complexes interspersed with corky tissue external to the vasculature of the mesocarp (Fig. 6I,J). *Hakea* fruits are dehiscent, but at maturity the two portions remain united at the base and attached to the plant stem. In many species the fruit has pronounced humps on the lateral faces resulting from secondary thickening of the pericarp (Filla, 1926; Johnson & Briggs, 1963; Barker et al., 1999). The periearp, whether significantly secondarily thickened or not, comprises stone cell complexes instead of radially arranged fibres adjacent to the ventral suture and external to the vasculature in the mesocarp (Fig. 6B). In these respects *Hakea* fruits differ from *Conchotheca*.

Fruits of *Buckinghamia* differ from those of *Grevillea* and *Conchotheca* in that the dorsal hinge line is longer than the ventral suture (Fig. 5Q,R). Moreover, in *Buckinghamia* the radially directed vaseular bundles of the middle and outer pericarp are themselves branched (Filla, 1926, fig.70f) as opposed to the unbranched radial

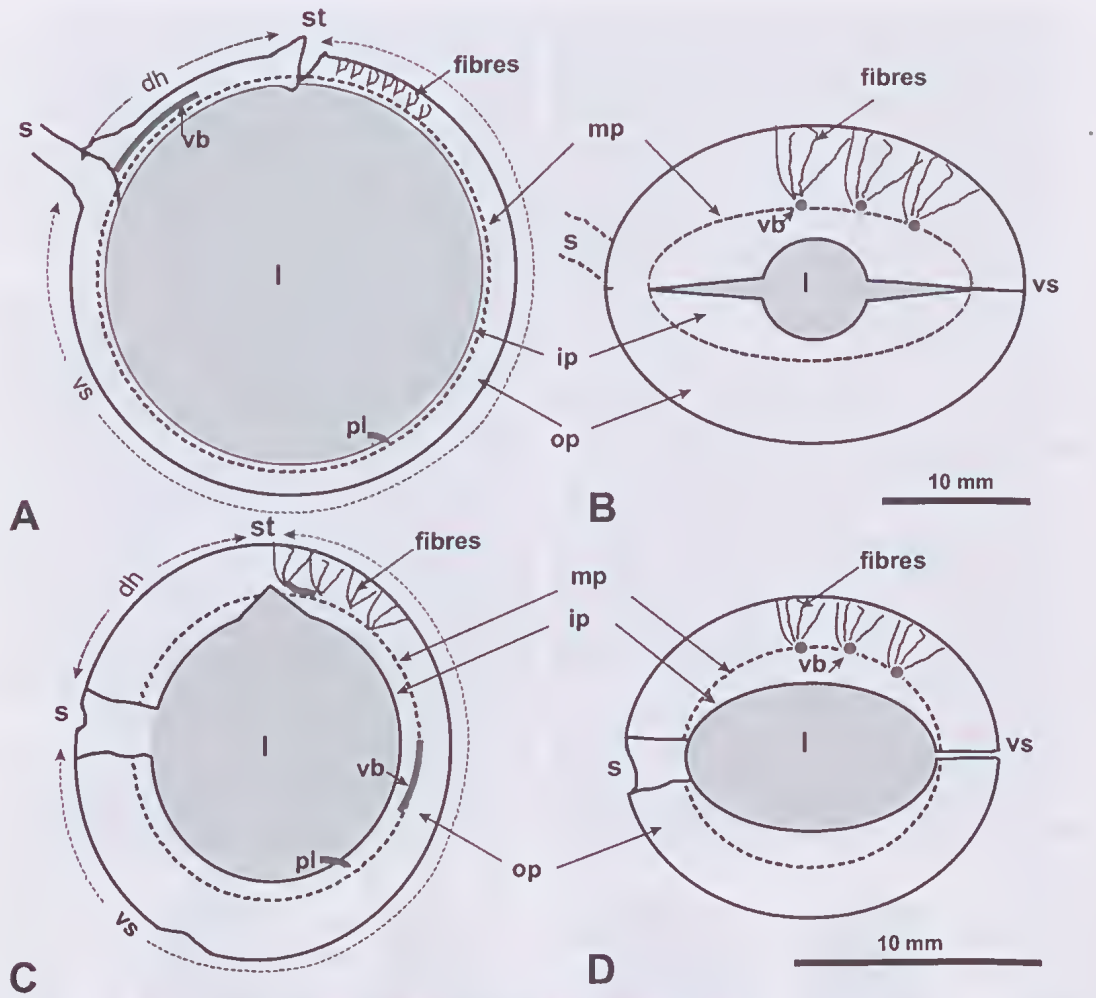
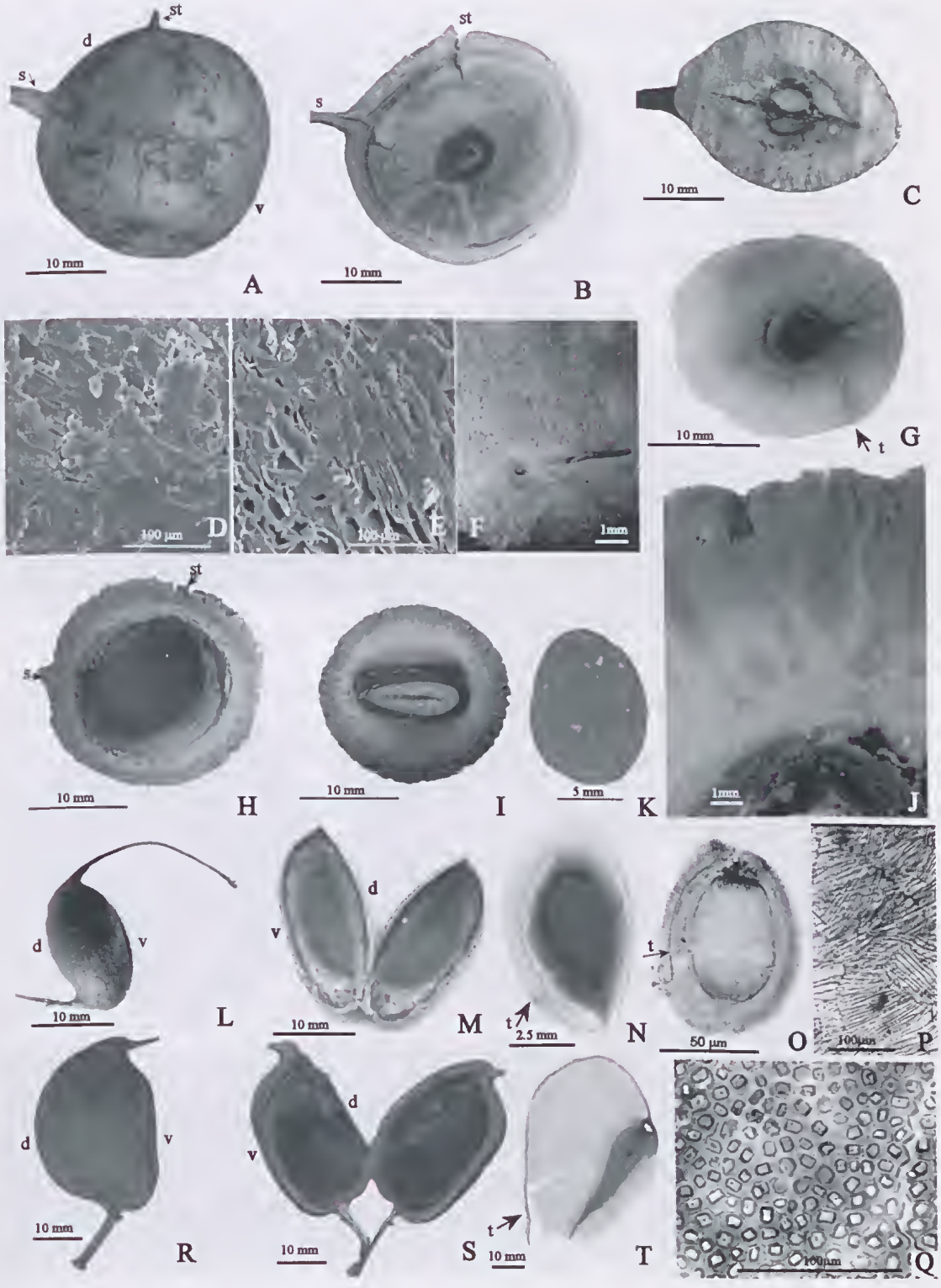



FIG. 4. Diagrammatic outline of longitudinal and transverse sections of fruit of *Grevillea heliosperma* (A,B) and holotype, NMVP53971, of *Conchotheca rotundata* (C,D); dh, dorsal hinge; l, loeule; ip, inner pericarp; mp, middle pericarp; op, outer pericarp; pl, placenta; s, stalk; st, stigma; vb, vascular bundle; vs, ventral suture. Note, fibres illustrated in upper right segment only.

FIG. 5 (facing). Fruits and seeds of *Grevillea* (A-Q) and *Buckinghamia* (R-T). A-G, *Grevillea heliosperma* R.Br. A,B, lateral views showing exterior of fruit (d, dorsal hinge, v, ventral suture) and interior of loeule containing winged seed, arrows indicate position of stalk (s) and stigma (st); C, section of fruit cut transverse to ventral suture and dorsal hinge line showing two winged seeds cut transversely; D-F, portion of pericarp in transverse section showing radially aligned fibres in middle and outer pericarp (D) and vasculature surrounded by fibres in mid regions of pericarp (E,F); G, winged seed showing raphe trace (t) and seed body. H-K, *Grevillea candicans* C.A.Gardner. H-I, longitudinal and transverse sections of fruit showing interior of loeule (s, stalk, st, stigma) and unwinged seeds cut transversely (note only one seed with embryo); J, transverse section of fruit wall showing radial structure of middle and outer regions of pericarp, parenchymatous inner pericarp, and underlying section of seed coat (darker layer); K, seed, lateral view. L, *Grevillea robusta* A.Cunn. ex R.Br. lateral view of fruit (d, dorsal hinge line, v, ventral suture). M,N,P, Q, *Grevillea hilliana* F.Muell. M, lateral view of interior of fruit (d, dorsal hinge, v, ventral suture); N, winged seed showing branched raphe trace (t); P, cells of loeule lining; Q, inner epidermis of testa with cells containing crystals of calcium oxalate. O, *Grevillea pteridifolia* Knight, hemitropous ovule showing ovule trace (t) passing through outer integument to chalaza and hypostase. R-T, *Buckinghamia celsissima* F.Muell. R,S, exterior and interior of fruit in lateral view (d, dorsal hinge, v, ventral suture); T, winged seed showing raphe trace (t) at margin of wing.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vasculature of *Grevillea* (Filla, 1926, fig. 70d; Fig. 5E,F) and *Conchotheca* (Figs 2G, 3A).

**Conchocaryon** F.Muell., 1879

TYPE SPECIES (by monotypy). *Conchocaryon smithii* F.Muell., 1879.

DIAGNOSIS (Mueller, 1879: 39). 'Fruit hard, oblique-ovate, considerably compressed, one-celled, almost smooth, dehiscent only along the anterior (ventral) margin, produced at the lower portion of the back into two acute ridges. Placenta narrow, dorsal in the cavity; its point of attachment to the seed about midway up at the dorsal inner angle of the pericarp. Seed solitary, ovate, turgid, filling the lower part of the cavity, extended at the summit into a flat short triangular appendage'.

REMARKS AND COMPARISON. The genus was proposed on the basis of one specimen and was distinguished from *Conchotheca* on its 'unsymmetrical form', the fruit bulbous in basal regions and tapering towards the apex (Mueller, 1879: 39). Further systematic evaluation of the taxon is precluded as neither the type specimen nor any subsequently collected material has been located. Illustrations of the type, *C. smithii*, (Mueller, 1879, pl. 17, figs 4-6; 1883, pl.17, figs 4-6; Fig. 3E-G herein) imply bilateral symmetry and a fruit wall thickest on basal areas of the valve faces.

**Conchocaryon smithii** F.Muell. 1879
(Fig. 3F-G)

HOLOTYPE (by monotypy). Mueller, 1879: 39; pl. 17, figs 4-6.

TYPE LOCALITY. Gulgong, New South Wales, or 'from a Victorian locality' (Mueller, 1879: 39); Middle Miocene (Gulgong) or uncertain (Victorian locality).

DESCRIPTION (after Mueller, 1879: 39). Fruit asymmetrical about lateral axes, bilaterally symmetrical about vertical plane that includes stalk, stigma and potential dehiscence line; ovate with base broader than apex; edge at ventral suture acute and obtuse at dorsal hinge line; vertical axis 20mm, lateral axes 10-12mm. Stalk scar inset at base; fruit wall ~ 2mm thick, composed of thick-walled (15µm thick) fibres and/or sclereids up to 75µm in diameter; surface slightly rough. Seed attached laterally, the seed body filling basal portion of cavity and with a short wing directed towards apex of fruit.

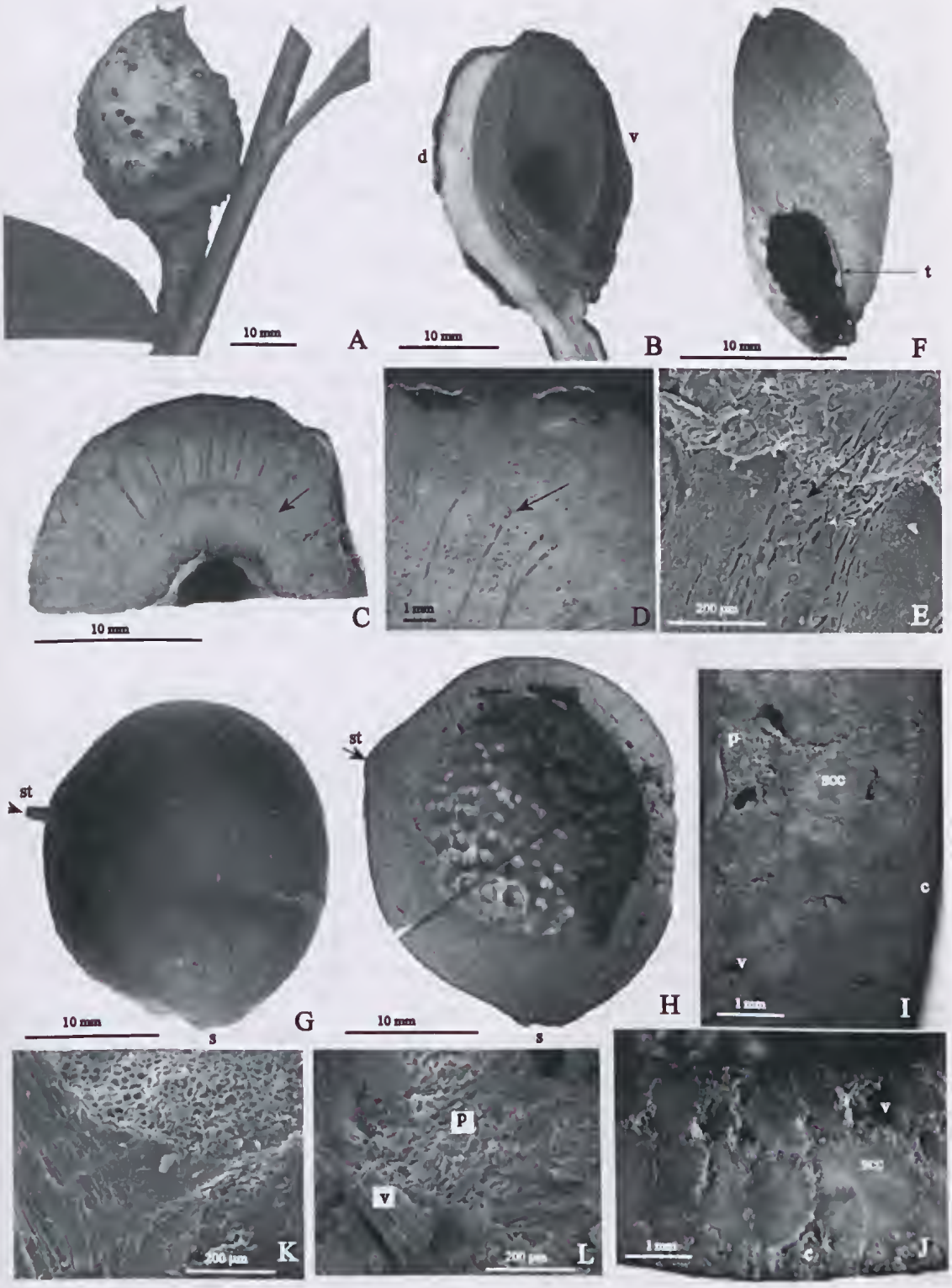
REMARKS. Characterisation of the species is based entirely on Mueller's description and illustrations, and is provided should specimens conforming to the holotype be located. Mueller (1879) introduced uncertainty as to the location of the described specimen; Gulgong is specified, and then qualified as possibly Victoria.

AFFINITY. With the Proteaceae (Tribe Grevilleeae) as suggested by Mueller (1879: 39), notwithstanding his suggestion the placenta is 'dorsal in the cavity'. Mueller compared the fossil with *Hakea* on the basis of the winged seed and woody fruit wall, which is swollen towards the base, but as noted by him, living species of *Hakea* possess two seeds, not one, as observed in the fossil.

## DISCUSSION

As suggested by Mueller (1873), *Conchotheca rotundata* is morphologically and anatomically consonant with fruits of the Proteaceae (Subfamily Grevilleoideae), and is more similar to those of *Grevillea*, Tribe Grevilleae than to other members of the family. Less certain is the detailed morphology and affinities of *Conchocaryon smithii*. Mueller (1879) believed the sole specimen resembled fruits of *Hakea* and to a lesser extent *Grevillea*, and an affinity with Tribe Grevilleeae is cautiously accepted on the basis of the original descriptions and illustrations. Thus, irrespective of uncertainties surrounding affinities of *Conchocaryon smithii*, the Tribe has a history in Australia that extends to at least the mid-Tertiary.

FIG. 6 (facing). Fruits and seeds of *Hakea* (A-F) and *Finschia* (G-L). A, *Hakea laurina* R.Br. lateral view; B-F, *H. actites* W.R.Barker; B, lateral view showing interior of locule showing abrupt demarcation between "dark" and "light" or secondary wood adjacent to dorsal hinge line (d) and stone cells at ventral suture (v); C, transverse section showing seed cavity (bottom centre), and sharp demarcation (arrow) between primary (inner darker zone) and overlying paler secondary wood of pericarp. D-E, detail of secondary wood showing libriform fibres (arrow) and overlying cork tissue; F, seed showing basal wing and raphe trace (t). G-L, *Finschia chloroxantha* Diels; G,H, lateral views showing exterior and interior of fruit, stigma (st), stalk (s); I,J, longitudinal and transverse sections of fruit wall showing stone cell complexes (scc), vasculature (v), parenchyma (p) and cork tissue (c); K,L, detail of vasculature (v) and parenchyma (p).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All records of the fossil fruits are from south-eastern Australia, but fossil leaves and pollen that may represent the Grevilleeae are known from other Australian localities in sediments of latest Cretaceous and Tertiary age (Fig. 1). The most securely founded identifications are of leaf compressions (*Maslinia grevilleoides* Blackburn) from the Middle Eocene of South Australia: these are similar in architecture and cuticular features to *Grevillea hilliana* Maiden, a northern Australian species (Blackburn, 1981). Less certain are the leaf impressions recorded from Vegetable Creek (Late Eocene), New South Wales, Melville Island (?Paleogene), Northern Territory, and Muradup (Late Eocene), south Western Australia each of which was likened to *Grevillea* (Deane, 1903; Pole, 1998a; McLoughlin & McNamara, 2001). Fossil pollen that is similar to that of *Grevillea exul* Lindl., a species endemic to New Caledonia, occurs in Maastrichtian sediments of the Otway Basin (as *Propylipollis* sp. B of Dettmann & Jarzen, 1996, 1998). *Grevillea*-and *Hakea*-type pollen referred respectively to *Hakeidites* (*Grevillea*) sp. and *Hakeidites (Hakea)* sp. by Macphail (1996) occurs in Miocene and younger sediments of the Murray Basin. To the north, in Papua New Guinea, Pliocene pollen attributed to *Hakeidites martinii* Khan, 1976 may represent the Tribe Grevilleeae. The fossil pollen was compared with pollen of extant *Hakea gibbosa* (Khan, 1976), but also resembles that of *Grevillea*.

There is no confirmed fossil record of the Grevilleeae from New Zealand. Fruits from the Pliocene near Auckland, and the Miocene of Otago were compared with those of *Hakea* (Moore &McKelvey, 1971; Pole, 1993, 1998b), but their morphological and anatomical characters are insufficiently known to verify this affinity. Similarly, the pollen taxon, *Proteacidites hakeoides* described by Couper (1960) from Eocene sediments of New Zealand, is insufficiently known to confirm identity with *Hakea*.

Fossils morphologically and anatomically congruent with Grevilleeae indicate that the Tribe was represented in Australia by latest Cretaceous (Maastrichtian) times and persisted, at least in southern areas, through the Tertiary to the present day. The majority of fossils have been allied with rainforest or monsoon forest representatives of *Grevillea* that today are restricted to northern parts of the genus' distribution range (Fig. 1). Fossils that may represent *Hakea* are unknown from pre-Miocene sediments, which may relate to lack of suitable habitats adjacent to depositional sites.

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## Appendix

## FRUIT AND SEED STRUCTURE IN THE GREVILLEEAE

### **Grevillea** R.Br.ex Knight (Figs 4,B, 5A-P)

Fruits of the majority of species are prolate ellipsoidal follicles. The majority of species (~265 spp.) contain seeds that lack a circumferential papery wing and of these most have a plump ellipsoidal seed body (Fig. 5K); two-seededness is the usual condition but one-seededness (by abortion) occurs in many species. A minority of species (~90 spp.) have a flat circumferential wing, and this is strongly associated with a flat seed body (Fig. 5G,N). The wingless, plump-seeded condition is typical of most species from the southeastern and south-western temperate regions of Australia, and is less common in the northern monsoon tropics and in the Eremaean, where winged-seeded species are more numerous. Fruits are borne on stalks that are lateral with respect to the stigma, with the ventral suture longer than the dorsal hinge line. Follicles and tardily dehiscent fruits are bilaterally symmetrical and split into equal portions along the ventral suture, but may remain conjoined along the dorsal hinge line adjacent to the stalk. The seeds are laterally attached and develop from hemitropous ovules (Brough, 1933).

*Pericarp*. Filla (1926) detailed development of follicles of *G. rosmarinifolia* A.Cunn. noting the progressive radial elongation and subsequent lignification of cells in the outer mesocarp between the outer epidermis and the vascular bundles; these lignified cells form a near continuous zone external to the longitudinally and laterally (tangential sensu Johnson and Briggs, 1975) aligned vascular bundles of the middle mesocarp (Filla, 1926, figs 36-38, 70d; Figs 4A,B, 5D-F). Cells of the inner mesocarp and the inner epidermis are tannin-filled and remain parenchymatous. This developmental pattern also has been observed by the authors in *G. hilliana* F.Muell., *G. pteridifolia* Knight, *G. banksii* R.Br. and *G. robusta* A.Cunn.ex R.Br. Mature follicles of these and other species investigated are characterised by fibre complexes of radially and longitudinally aligned components that cap the vascular bundles and radiate towards the external surface of the pericarp which has a smooth, rough, or hair encrusted surface (Filla, 1926). The inner mesocarp between the inner epidermis and vascular bundles consists predominantly of parenchyma, the cells of which may be tannin infilled as in *G. heliosperma* R.Br., *G. robusta*, and *G. candicans* (Fig. 5F,J).

*Seeds*. Seeds of *Grevillea* are winged, rimmed, or wingless. The wing, if present, is situated in the plane of flattening of the seed (ie. the plane that includes the hilum, chalaza, and micropyle) and encircles or forms a partial border to the exotesta around the embryo sheath (Fig. 5G,N). In *G. robusta*, the wing and exotesta, which surrounds the embryo sheath, develops from the outer epidermis of the outer integument, and through it passes the ovule trace, which branches dichotomously near the margin of the wing (Fig. 5N). One branch passes through the raphe to the chalaza, and the other branch passes in the opposite direction and terminates within the wing (Brough, 1933). The inner epidermis of the outer integument is a prismatic layer (Brough, 1933); the cells of this, the crystal layer (Fig. 5Q), contain calcium oxalate crystals, which are laid down in the developing ovule 2-3 weeks after anthesis in species examined. At this stage of development, the inner integument disintegrates, except for the cuticles separating it from the outer integument and the nucellus. These two cuticles form the embryo sheath, in which the micropyle is situated (Fig. 5N). This developmental pattern has been confirmed by us for the winged seeds of *Grevillea heliosperma*, *G. pteridifolia*, *G. banksii* and *G. hilliana*. The elaborate ruff-like structure that forms the wing about the margin of *G. hookeriana* seeds is located on their topologically inner surface. Mature seeds are non-endospermic.

*Remarks*. In all species examined the raphe is branched near its point of entry in the marginal wing or rim; the branch traces are opposed, the main branch directed towards the chalaza, the other in the opposite direction where it terminates within the wing or rim (Fig. 5N). The palisade layer described by Brough (1933) in the seeds of *G. robusta* consists of a single layer of cells containing crystals of calcium oxalate. Seeds of other species examined possess a crystal layer, which comprises transfer cells in which calcium oxalate crystals or granules accumulate (Fig. 5Q; Léon et al., fig. 8). This layer invariably develops from the inner epidermis of the outer integument in *Grevillea* and other taxa of the Proteaceae (Netolitzky, 1926; Manning & Brits, 1993; Stroschen, 1986a,b,c; Clifford & Dettmann, 2005).

**Hakea** Schrad. & J.C.Wendl. (Fig. 6A-F)

Fruits of *Hakea* are woody, tardily dehiscent, modified follicles usually containing 2 winged-seeds. The follicles are prolate ellipsoidal, subspheroidal or spheroidal, often with a beak or paired horns at or near the apex (Fig. 6A); they split fully or partly down the ventral or both sutures into equal portions, the ventral suture being shorter than the dorsal hinge line (Fig. 6B). The follicles are secondarily thickened, the thickening greatest on the faces of the valves and adjacent to the dorsal hinge line (Fig. 6B); surface is smooth or variously sculptured, and the outer bark may break away from the underlying mesocarp. The seeds are laterally attached near the base of the follicle and develop from hemitropous ovules (Kausik, 1949; Venkato Rao, 1971; Johnson & Briggs, 1975; Barker et al., 1999).

*Pericarp.* Filla (1926) traced pericarp development in *Hakea suaveolens* R.Br. (=*Hakea drupacea* C.F.Gaertn.) Roem.&Schu. and *H. microcarpa* R.Br., noting that after initial primary growth of the mesocarp vasculature and radial elongation of stone cells between the vasculature and the epidermis, there is considerable enlargement of the follicle resulting from secondary growth generated from a fascicular and interfascicular cambium layer (Filla, 1926, figs 41-45; fig. 6C-E herein). The pale secondary wood is generated from the interfascicular cambium and rows of libriform fibres from the vascular cambium; a meristem external to the secondary wood and beneath the epidermis generates cork tissue, which may abscise at maturity. The boundary between the primary and secondary wood is expressed as a sharp demarcation between the layers of dark and pale wood exposed in open follicles (Fig. 6B). Dark wood surrounds the seed cavity and forms the mesocarp at the ventral suture; pale wood overlies the dark wood about the dorsal hinge line and may envelop the dark wood except along the ventral suture, or it may be limited to regions immediately adjacent to the dorsal hinge line. The width and surface extent of the pale wood zone is taxonomically significant for discriminating between some taxa (Barker et al., 1999).

*Seeds.* Seeds of *Hakea* are winged, the wing terminal or more rarely at one side or encircling seed body, which is convex on the face adjacent to the seed cavity of the follicle and flattened on the other surface (Fig.6F). Wing situated in the plane of flattening of the seed (ie. the plane that includes the hilum, chalaza, and micropyle); develops from basal tissues of ovule (Kausik, 1949). The ovule trace from the hilum passes through the outer integument and radiates into the tannin-rich hypostase near wing base. Seed coat often sculptured on convex surface, exotestal; comprising outer layer that develops from outer epidermis of outer integument and an inner crystal layer of transfer cells that contain crystals of calcium oxalate and derive from the inner epidermis. These surround the embryo sheath in which the micropyle is situated and is formed as in *Grevillea* from cuticles between the outer integument and the embryo. Mature seeds are non-endospermic.

*Remarks.* The woody follicles of *Hakea* are unique in the Proteaceae in possessing secondary wood. Seed development was detailed by Kausik (1949), who, although not recognising the presence of calcium oxalate, noted tearing of tissues during attempts to section developing ovules of *Hakea saligna* Knight.

**Finschia** Warb. (Fig. 6G-L)

Fruits of *Finschia* are tardily dehiscent subspheroidal or ellipsoidal follicles borne on lateral stalks and contain 2 wingless seeds (Fig. 6G,H). The fruits are bilaterally symmetrical about the dorso-ventral plane and the seeds are laterally attached. Pericarp and seed morphology/anatomy was briefly outlined by Sleumer (1955) and Johnston & Briggs (1975); mature fruits of *F. chloroxantha* Diels have been investigated herein.

*Pericarp.* Mature pericarps of *F. chloroxantha* have large stone-cell complexes that cap the vascular bundles and radiate towards the smooth external surface (Fig. 6I,J). Between the stone-cell complexes are thin-walled, isodiametric parenchymatous cells; parenchymatous cells also occur in inner regions of the pericarp, whereas the outer regions comprise corky tissue (Fig. 6K,L).

*Seeds.* Seeds are flattened and wingless, but almost encircled by the raphe, which branches near its entry into the chalaza. The exotesta comprises tannin filled thick-walled cells that overlie a layer of pentagonal cells containing crystals of calcium oxalate. The underlying embryo sheath in which the micropyle is situated comprises two cuticles as in seeds of *Grevillea* and *Hakea*. The mature seeds are non-endospermic.

*Remarks.* Fruits of *Finschia chloroxantha* differ from those of *Grevillea* in possessing large clusters of stone-cells in the middle and outer parts of the pericarp and wingless seeds.

**Buckinghamia** F.Muell. (Fig. 5R-T)

This genus belongs to the tribe Embothrieae and comprises two species endemic to northeastern Queensland. Fruits and seeds examined are from the type species, *B. celsissima* F.Muell., which has fruits similar to those of *B. ferruginiflora* Foreman & Hyland, except they are smaller. Fruits are prolate ellipsoidal follicles containing 4 winged-seeds that develop from hemitropous ovules with near basal attachment.

*Pericarp.* Mature follicles are bilaterally symmetrical about the vertical plane including the pedicel, dorsal hinge line and ventral suture; ventral suture shorter than the dorsal hinge line (Fig. 5R,S). Pericarp wall predominantly of mesocarp with longitudinal, lateral, and third-order radial vasculature, the bundles mostly capped by radially aligned fibres and sclereids interspersed with tannin-filled parenchyma. The inner mesocarp between the inner epidermis and vascular bundles is predominantly of tannin-filled parenchymatous cells.

*Seeds.* Seeds have near-basal attachment, are near-rhomboidal and flattened in shape, and have a marginal wing in the plane that includes micropyle, chalaza and raphe (Fig. 5T). Raphe trace marginal to wing, extending from hilum to chalaza where the vascular bundle branches and radiates into hypostase. Outer epidermis of testa, which develops from the outer epidermis of the outer integument, is composed of loose tannin-filled isodiametric sclereids and parenchyma that separate from seed coat at maturity. Inner epidermis of testa develops from inner epidermis of outer integument, and is composed of isodiametric pentagonal-hexagonal cells each with a prismatic crystal of calcium oxalate. The crystal layer forms the wing and envelops seed sheath, which consists of two cuticles, the outer derived from inner epidermis of inner integument and the inner from that of the nucellus. The seeds are non-endospermic.

*Remarks. Buckinghamia* follicles superficially resemble those of some *Grevillea* species, but differ in possessing branched lateral vascular bundles in the mesocarp and a ventral suture shorter than the dorsal hinge line. In mature *Buckinghamia* seeds loose sclereids of the outer testa are shed, whereas in *Grevillea* seeds the outer testa that envelops the crystal layer and embryo sheath is retained.

# NEW GENERA AND SPECIES OF SMALL TICKING AND 'CHIRPING' CICADAS (HEMIPTERA: CICADOIDEA: CICADIDAE) FROM QUEENSLAND, WITH DESCRIPTIONS OF THEIR SONGS

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Five new genera of small cicadas (<15 mm total body length), including nine new species, are described, all assigned to the Cicadidae, Tibicininae, and Tribe Cicadettini. The genera are *Crotopsalta*, *Gagatopsalta*, *Caliginopsalta*, *Pipilopsalta* and *Drymopsalta*. The new species are *Crotopsalta plexis*, *C. fronscecetes*, *C. strenulum*, *C. poaecetes*, *G. auranti*, *G. obscurus*, *Caliginopsalta percola*, *P. ceuthoviridis*, and *D. crepitum*. Descriptions, distribution, behaviour and songs are provided for each genus and species. The *Crotopsalta* species are characterised by simple ticking songs, differing with respect to their pulse repetition rates and pulse structures between species. Increasingly complex chirping songs, comprising short echemes containing multiple pulses, characterise the *Caliginopsalta* and *Pipilopsalta* songs. Even more complex temporal patterning and structure of the chirp echemes characterise the *Gagatopsalta* and the *D. crepitum* songs, the latter exhibiting a remarkable series of song patterns. □ *Ticking cicadas, chirping cicadas, Queensland, songs, Cicadidae.*

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The Australian cicada fauna is not well documented. There are many known but still undescribed species in museums and private collections and many new species are still being collected. Current taxonomic research is addressing the overdue higher systematics of cicadas in general, and in particular clarifying and extending the generic classification of Australian species (Moulds, in press). Apart from their inherent importance in species recognition, cicada songs are valuable tools taxonomically. In the field, they provide excellent means for identification of known species and recognition of new species and species complexes. Songs are species specific, with many Australian and overseas examples now documented (e.g. Myers, 1929; Alexander & Moore, 1958; Young, 1972; Ewart, 1988, 1989, 1998; Ewart & Popple, 2001; Popple, 2003; Simões *et al.*, 2000; Sueur, 2002).

This work stems from the recognition, in Queensland, of small and inconspicuous cicadas emitting soft and apparently simple ticking songs, as well as other small species emitting slightly more complex chirping songs. The field recognition of these songs has been greatly aided by use of a bat detector. Detailed descriptions of these songs are provided, based on field and laboratory sound recordings. Although sharp chirping songs are known in species belonging to several described genera, this work describes five new genera (Table 1) containing nine previously undescribed species.

ABBREVIATIONS. Repositories: ANIC, Australian National Insect Collection, Canberra; AE, private collection of A. Ewart; BMNH, The Natural History Museum, London; LWP, private collection of L.W. Popple, Brisbane; MSM, private collection of M.S. Moulds, Sydney; QM, Queensland Museum, Brisbane; UQIC, The University of Queensland Insect Collection. The following abbreviations apply to the paratype data: Ck, Creek; HS, Homestead; Hwy, Highway; jct, junction; L, Lake; NP, National Park; Pty, property; Ra, Range; Rd, Road; Rec, recorded (= aural/electronic song recording); R, river; SF, state forest; sp, species; spec, specimen; Stn, Station (HS); xing, crossing; CB, C. Burwell; DC, D. Cook; GD, G. Daniels; SE, S. Evans; AE, A. Ewart; RBL, R.B. Lachlan; CL, C. Lambkin; SL, S. Lamond; RM, R. MacSloy; SM, S. McEvey; GBM, G.B. Monteith; GB&SRM, G.B. & S.R Monteith; JM, J. Moss; MSM&BJM, M.S. & B.J. Moulds; JN, J. Nowland; LWP, L.W. Popple; LW&RP, L.W. & R. Popple; IR, I. Rattray; DMR, D.M. Reeves; JS, J. Skevington; MAS, M.A. Schneider; RS, R. Stoodley; AS, A. Strange; AW-H, A. Walford-Huggins; SW, S.

TABLE 1. Summary of selected morphological characters, for males only, distinguishing the five genera described

| Genera: | *Crotopsalta* | *Gagatopsalta* | *Caliginopsalta* | *Pipilopsalta* | *Drymopsalta* |
|---|---|---|---|---|---|
| **Abdomen:** shape (in dorsal view): | Evenly tapered distally | Cylindrical, gentle tapered distally | Evenly tapered distally | Tending rounded, bulbous in dorsal and lateral profile | Slender and evenly tapered distally |
| **Rostrum:** Extends to: | Mid coxae | Between mid and hind coxae | Hind coxae | Mid coxae | Hind coxae |
| **Fore wing:** Lengths of apical cells compared to ulnar cells: | Approximately equal. | Approximately equal. | Approximately equal. | Mostly shorter than ulnar cells. | Approximately equal. |
| Costal vein; anterior curvature proximal to node: | Gently curved | Gently curved | Gently curved | Minimal curvature | Marked anterior curvature |
| **Hind wing:** Apical cells: | 6 | 6 | 6 | 6 | 5 to 6 (rarely 4) |
| Hindwing: Infuscation: | None | None | Brown infuscation within plaga and anal lobe | None | None |
| **Operculae:** shape: | Moderately elongated, rounded along distal margin; marked ridge. | Weakly elongated, rounded along distal to medial margins; marked ridge. | Rounded along distal and medial margins; gently domed and ridged | Broadly rounded along medial-distal margins; gently domed and ridged. | Moderately elongated with oblique, blunt to variably rounded distal margin. |
| Operculae: Separation of inner margins : | Clearly separated | Clearly separated | Clearly separated | Separated but closely spaced | Clearly separated |
| **Timbals:** Long ribs; Ribs fused ventrally: Ribs fused to basal spur: | 4; rib 5 shortened in length<br>1 to 3 (± 4)<br>1 to 4 | 5<br>1 to 2<br>1 to 3 | 5; rib 4 discontinuous.<br>1 to 4<br>1 to 3 | 5; ribs 4 and 5 shortened.<br>1 to 2<br>1 to 2 | 4 to 5; ribs 4 ± 5 shortened.<br>1 to 3<br>1 to 4 |
| **Pygofer:** Shape (dorsal view): | Broadly pyriform | Ovoid. | Ovoid. | Ovoid. | Ovoid to roughly rectangular. |
| Pygofer: Uncal lobes: | Extended orthogonally, thickened and rounded apically | Sharply terminated and extended. | Curved, anteriorly pointing and sharply terminated. | Extended steeply, subacute and curved. | Extended orthogonally, thickened and rounded apically. |
| Pygofer: Upper lobes: | Triangular, pointing steeply ventrally, rounded apically | Prominent, extended distally and apically rounded. | Prominent, rounded apically | Rounded and not strongly extended | Moderately extended, subacute, rounded apically. |
| Pygofer: Lower lobes: | Clearly defined and rounded. | Partly hidden (in lateral view) | Small and rounded | Rounded, slightly elongated. | Well developed, rounded apically. |
| Pygofer: Inner lobes: | Not developed. | Rounded, extended ventrally | Not developed. | Visible, subacute, but not prominent (in lateral view) | Not developed. |
| Pygofer: Beak: | Inconspicuous to absent. | Prominent and rounded. | Moderately developed, clearly visible. | Prominent and rounded. | Conspicuous, sharply defined in lateral profile. |

Wright, FRW, F.R. Wylie; DY, D. Yeates. Other abbreviations used in the main text are: BL, total body length; FWL, fore wing length; HW, head width; PW, pronotum width; AW, abdomen width; FWL/BR, fore wing length/breadth ratio.

## MATERIALS AND METHODS

The anatomical terminology follows Moulds (1990; in press) and Duffels (1977) for general body and wing characters; Duffels (1977), Dugdale (1972), and Moulds (2003) for genitalia; de Boer (1999) for operculae, and Simmons & Young (1978), Dugdale (1972) and Bennet-Clark (1997) for timbals. The timbal long ribs are referred to sequentially as ribs numbered 1-4 (±5), with rib 1 being the most posterior rib (i.e. adjacent to the timbal plate).

Measurements (in mm) are given as ranges and means (in parentheses) of a subset of specimens from each species, including the smallest and largest available specimens. The head width is

taken across the outer margins of the compound eyes; pronotum width is the maximum measured width; the abdomen is measured across the auditory capsules. The fore wing length/breadth ratios are based on maximum measured values of each parameter for each fore wing.

## SONG RECORDINGS AND ANALYSES

Non-field recorded songs were made, using metal tapes, with a Sony Walkman cassette recorder WM-D6C model, in conjunction with a Sennheiser microphone model K6/ME66. The recorder has a linear response to 15 kHz, and responds to approximately 18 kHz. These recordings were performed with single insects within plastic containers, 16.5x16.5x9.5 cm, in which small quantities of the relevant vegetation were inserted on which the insects were captured. A fine white cloth covering was placed over the top of the boxes, with lighting immediately above, and the microphone placed on the top edge of the box. Reverberation effects have not been observed in the resulting songs recorded, at least within the limits of resolution of the recordings. Near-field effects are a possible complication of using the relatively small recording boxes, and could be significant at frequencies of ≤5kHz. These are, however, lower than the main frequency ranges emitted by the ticking cicadas. For the same reason, possible proximity effects are not considered to be significant. The primary reasons for using the containers are that, for the very small and mostly very wary cicadas, it is usually not feasible to place a microphone close enough, for long enough, to individual insects to directly record their low amplitude songs in the field. The most notable exception is *Pipilopsalta ceuthoviridis* sp. nov. In the containers, they can be readily induced to sing in strong, artificial lighting (not fluorescence), and with minimal background noise. The lighting also provides heat; temperatures in the boxes are consistently 30-35°C during normal summer recording sessions.

Field recordings were made through bat detectors (Mini-2 and Mini-3 ultra sound Advice models, U.K.), that were also routinely used to detect the ticking songs in the field. The primary aim of these recordings was for determining tick rates, but they have the advantage of being able to confirm the ability of the essential pulse structures to survive propagation in various field environments, the recordings typically made 2-30m from singing insects. Songs of *P. ceuthoviridis* n.sp. were recorded in the field with the WM-D6C cassette recorder, as well as in containers.

Computer analyses were performed by initial digitising through a 16-Bit Terratec sound card at 44.1 kHz sampling frequency, followed by processing with Avisoft SASLab Pro 4 software. These data are stored in a library of mostly Queensland cicada songs held at the Queensland Museum.

A modified terminology of Ragge & Reynolds (1998) is adopted for descriptions and analyses of the songs, with the exception of the *Crotopsalta* ticking cicadas, where the term 'pulse' is considered most appropriate. Although the Ragge & Reynolds terminology was designed for orthopteran insects, there are sufficient similarities in essential song structures to justify extending the terminology to the cicada songs herein. The term ***syllable*** is used for discrete but relatively short (≤20ms) pulse groups that plausibly result from a single buckling movement (in±out) of one or both timbals. The latter may result from alternate buckling of the timbal pairs, or synchronous buckling of both timbals, but implies no significant intervening time gap within the resulting syllable. The term ***echeme*** is applied to the first order assemblage of syllables produced during the continuous buckling of the timbals pairs (i.e. ≥2 cycles of buckling without significant pause). Time expanded waveform and envelope plots reveal that the syllables are usually resolved into smaller (higher frequency) 'syllable-like' groupings termed ***hemisyllables***, plausibly resulting (at least in part) from the buckling ('clicking') of individual timbal ribs. In most songs of the smaller cicadas, the hemisyllables can be further resolved into shorter (higher frequency) ***pulses***, representing the fundamental frequency carrier waves of songs.

## SYSTEMATICS

Family CICADIDAE Leach
Subfamily TIBICININAE Atkinson
Tribe CICADETTINI Buckton

### Crotopsalta gen. nov.

TYPE SPECIES. *Crotopsalta plexis* sp. nov.

INCLUDED SPECIES. *C. plexis* sp. nov.; *C. fronsecetes* sp. nov.; *C. strenulum* sp. nov.; *C. poaecetes* sp. nov.

ETYMOLOGY. Greek *croto,* a tick/rattle; -psalta is a generic ending that is sometimes used for the Cicadidae.

DIAGNOSIS. Very small, ~9-15 mm total body length, characterised by sharply defined and

relatively simple ticking songs. Head and thorax of similar width with abdomen relatively narrow and evenly tapered distally (as viewed dorsally); sternites rounded, projecting below tergites in lateral view. Compound eyes clearly separated, along their outer ventral margins, from pronotum; distance between lateral ocelli similar to distance between lateral ocellus and eye. Width of head (including eyes) slightly greater than width of pronotum across lateral margin. Width of pronotum measured from lateral margins similar to width of mesonotum between fore wings; lateral margins of pronotal collar weakly to moderately ampliate and outwardly curved. Rostrum extends to, but not beyond mid coxae. Wings hyaline with no infuscations. Fore wing relatively short and broad with length/breadth ratios in range ~2.3-3.0; red-brown to brown pterostigma; costal vein more or less even in width to node, with only slight thickening at node; costal vein gently curved anteriorly proximal to node; selcrotised area anterior to costal vein very narrow and much thinner than costal vein thickness; intersection of CuA-M veins approximately midway along first vein segment section (proximal to basal cell) of M vein that forms inner margin of radial cell; the distal vein sections along M forming the inner radial cell margin not all of similar length; eight apical cells; apical cells more or less similar in length, overall, to ulnar cells (some shorter, some longer). Hind wing with six apical cells. Operculae moderately elongated parallel to abdomen with weak ridge extending from distal through to basal areas; distal margins broadly rounded; inner margins of operculae widely separated; meracantha located strongly asymmetrically proximal to medial margins of operculae. Timbals with four long ribs and reduced fifth rib, the ribs 1-3 extensively fused ventrally; ribs 1-4 fused dorsally to the distinct basal spur; four (less often three) short ribs; narrow dome on timbal plate; part of the anterior margin of the white resilin area of timbal is markedly deflected outwards into a dome-like outline. Pygofer broadly pear-shaped (pyriform) in dorsal view; uncal lobes steeply ascending as seen in lateral view, thickened and rounded apically; upper lobe roughly triangular, pointing steeply ventrally, terminally rounded to relatively acutely rounded; lower lobe clearly defined and rounded; inner lobes not clearly developed; beak inconspicuous to absent; median process small (relative to uncal lobes); trifid aedeagus with a pair of sclerotised dorsal pseudoparameres longer than sclerotised ventral support, and unsclerotised endotheca.

## KEY TO SPECIES OF *CROTOPSALTA*

1. Operculae with brown to black colouration, sometimes patchy and restricted along lateral margins and basal areas; auditory capsules black, dark brown centrally.....2

   Operculae uniformly pale sandy brown, with or without minor pale brown around crest on dorso-lateral margins; auditory capsules usually pale brown to sandy brown with or without thin dark brown to black margins (rarely entirely dark brown to black).....3

2. Sternites pale to medium reddish brown (rarely fawn colour); tergites 3- 4 (±5) with or without pale brownish lateral patches; distal margin of opercula does not extend to anterior paramedial margin of sternite II.....*plexis*

   Sternites pale to medium brown; tergites 3 - 6 (±7) with well defined black to dark brown patches; distal margins of operculae extend to anterior paramedial margin of sternite II .....*fronsecetes*

3. Sternite II with small black patch medially; auditory capsules pale to medium brown with thin black to dark brown margins; dark brown to pale brown irregular patches laterally on tergites 3-7; distal margins of operculae extend to anterior paramedial margin of sternite II; timbal long ribs 1-4 fused ventrally.....*strenulum*.

   Sternites without black medial marking; auditory capsules uniformly sandy brown (occasional small brown marking adjacent to central areas); no darker lateral colouration on tergites; distal margins of operculae do not extend to anterior paramedial margin of sternite II; timbal long rib 4 not fused ventrally with ribs 1-3; meracantha very reduced in size and rounded.....*poaecetes*

Note: The number of separate characters listed for each step is a reflection of the inherent variability within each species. Single characters, taken alone, may not be diagnostic.

### **Crotopsalta plexis** sp nov..
### (Figs 1, 2, 7-11, 36, Table 2)

*Notopsalta* sp. I: Ewart, 1998: 65, 66, figs 19A, 13B.

MATERIAL. HOLOTYPE ♂, QMT99209, Hubbards Pty. Miles, S.Qld., Large wilga shrubs, 26°09.143'S 150°20.237'E, 28 Sept 1997, AE.

PARATYPES: SOUTH AND CENTRAL QUEENSLAND: 1♂, Brigalow Res. Stn. nr. Theodore, AE; 28.x.2000, 24°49.47'S 149°48.05'E; 1♂, As previously, Rec; 1♂, Brigalow Res. Stn. nr. Theodore, AE, 27.x.2000, 24°49.47'S 149°48.05'E, Rec; 1♂, 1♀, Glebe Weir, 30 km NE Taroom, 2.x.99, AE, 25°27.85'S 150°02.00'E'; 1♂, Glebe Weir, 30 km NE Taroom, 2.x.99, AE, 25°27.85'S 150°02.00'E, Rec; 2♂, 21km N. Wandoan, AE, 3.x.99, mixed brigalow, 25°56.74'S 149°54.14'E; 1♂, As previously, Rec(spec 1); 1♂, As previously, Rec(spec 2); 1?, 1 km W. Morven, 4.x.99, AE, 26°24.68'S 147°06.16'E; 1♂, As previously, Rec; 1?, 16

km E. Roma, AE, wilga, 7.x.99, 26°34.78'S 148°56.95'E; 6♂; 1km W. Morven, AE, 6.x.99, 26°24.68'S 147° 06.16'E; 1♂, As previously, Rec; 1♂, 1km W. Morven, *Casuarina*-brigalow, 2 Sept 2000, AE, 26°24.75'S 147°06.26'E, Rec(spec 1); 1♂, As previously, Rec(spec 2); 1♂, Brigalow Res. Stn., nr. Theodore, N.W. brigalow section, 21.xii.2000, AE, 24°47.92'S 149°45.45'E, Rec; 1♂ 45km N. Roma, myall, 15.xii.2000, AE, IR, 26°11.83'S 148°42.23'E, Rec; 1♂, Muckadilla, nr. School, grass, 16.xii.2000, AE, 26°35.25'S 148°23.19'E; 1♂, 29km E. Goondiwindi, 16.i.2001, AE, brigalow woodland, 28°29.71'S 150°32.82'E; 5♂, 2♀, Hubbards Pty, Chinchilla, 26°09.143'S 150°20.237' 30.i.98; 1♂, 28km S.E. Goondiwindi, 17.i.2001, AE, 28°38.77'S 150°32.98'E, Rec; 2♂, Hubbards Pty. Miles, large wilga shrubs, 26°09.143'S 150°20.237'E, 28.ix.1997; 1♂, Barakula SF, nr. Chinchilla, virgin brigalow, 15.xii.1997, 26°14.42'S 150°48.86'E, AE; 2♀, Mt. Lawnton, 16 km S. Wandoan, on *microcitrus* sp., 23.ix.1990, DMR; 2♂, 12♀, Mt. Lawnton, 16 km S. Wandoan, on *Capparis* sp., 30.ix.1990, DMR; 1♂, 6.1 km E. Kaimkillenbun, AE, 23.xii.2001, 27°04.35'S 151°29.83'E, Rec; 1♂, 16 km E. Roma, 25.xi.1999, AE, *Eremophila mitchellii*, 36°34.80'S 148°56.97'E; 1♂, 44.1 km S. of Theodore, 20.xii.1999, AE, brigalow, 25°14.51'S 149°57.232'E, Rec; 1♂, 41 km WSW Banana, brigalow, AE, 29.xii.2002, 24°37.08'S 149°46.24'E, Rec; 1♂, 14.6 km W. of Drillham, brigalow, 26.x.1998, AE, 26°38.65'S 149°49.94'E; 1♂, 15.6 km N. Taroom/Warrego Rd. jct, N. Miles, AE, brigalow, 17.x.1998, 26°31.64'S 150°07.50'E, Rec; 3♂, Muckadilla, near State School, grass, AE, 2.ii.2000, 26°35.31'S 148°23.19'E; 1♂, As previously, Rec; 1♂, 16 km E. Roma, Blythsdale South Rd., *Eremophila mitchellii*, AE, 2.ii.2000, 26°34.81'S 148°56.98'E; 1♂, brigalow, 1 km E. Brigalow Township, AE, 22.xii.2001, 26°50.94'S 150°47.83'E; 1♂, 31 km W. Mitchell, brigalow, *Cassinia*, *E. mitchellii*, AE, 12.i.2002, 26°28.74'S 147°40.37'E, Rec; 1♀, Glebe Weir, Taroom, 25°27.83'S 150°01.99'E, 29.ix.1997 **(AE)**. 1♂, Brigalow Res. Stat., WNW Theodore, 5-12.xii.1999, JM, LWP, 352-000*; 3♂ 1♀, Coolmunda Dam via Inglewood, 15.xii.2001, LWP, RM, minidisc, 352-0004, 0007 to 0009; 2♂, 2♀, Glebe Weir, nr. Taroom, 4-5.xii.1999, JM, LWP, MV lamp, 352-0002, 0001, 0004, 0003; 1♂, 1♀, Tara Shire, 47 km SW Dalby, 27.xii.2001, LWP, AS, 352-0011, 0010; 1♂, NNW Roma, 26°12'41"S 148°42'02"E, C. Eddie, 20.x.2001, 352-0012;

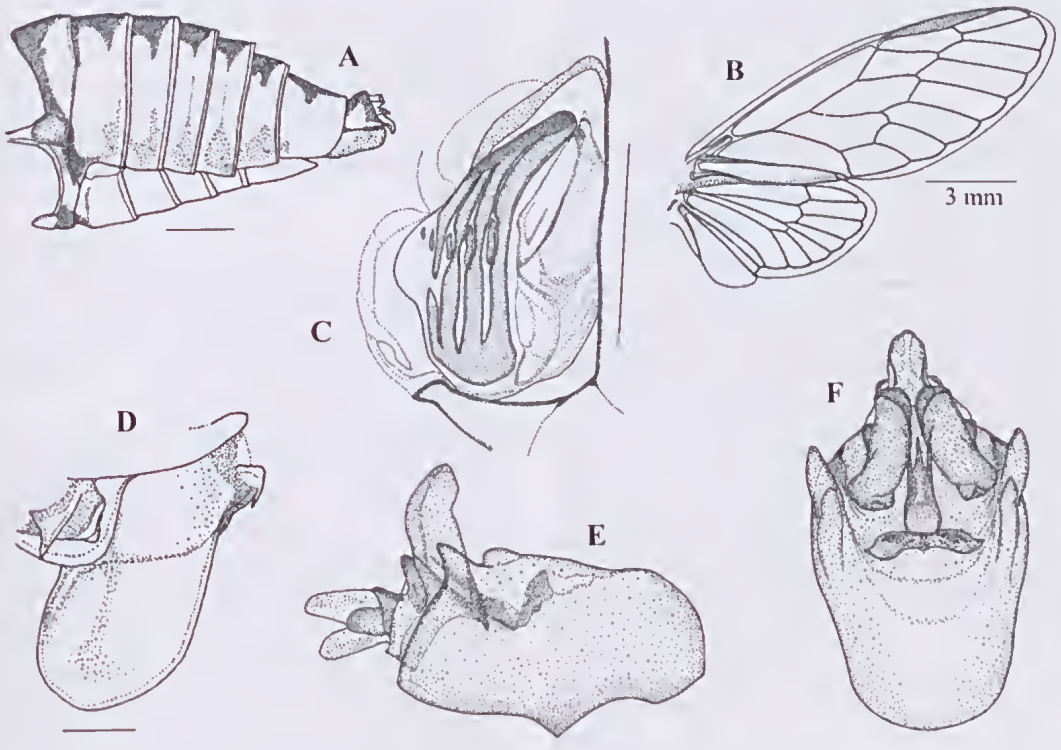


FIG. 1. *Crotopsalta plexis*. A, Lateral abdomen view; B, fore and hind wings; C, timbal; the right-hand edge as shown represents the posterior margin, the top the dorsal edge; D, opereula; E, and F, lateral and ventral views of pygofer. ). Length of pygofer 1.7mm. Scale bars =1mm exeept wings (3mm). Drawings based on speeimen from near Chinchilla, SEQ.

1?, as previously, 11.x.2001, 352-0013 **(LWP)**. 1♂, 1♀, 25°31'S x 150°03'E, Boggomoss No. 10, via Taroom, 14.xi.1996, DC, at Light. 065 **(QM)**. 1♂, Hubbards Pty, Chinchilla 26°09.143'S 150°20.237', 30.i.98; 1♀, Mt. Lawnton, 16 km S. Wandoan, *microcitrus* sp., 23.ix.1990, DMR **(BMNH)**. 1♂, 44.1 km S. of Theodore, 20.xii.1999, AE, brigalow, 25°14.51'S 149°57.232'E; 1♀, Mt. Lawnton, 16 km S. Wandoan, on *Capparis* sp., 30.ix.1990, DMR **(ANIC)**. 1♂, 1 km W. Morven, *Casuarina*-brigalow, 2.ix.2000, AE, 26°24.75'S 147°06.26'E; 1♀, Mt. Lawnton, 16 km S. Wandoan, on *microcitrus* sp., 23.ix.1990, DMR **(MSM)**.

* These refer to the numerical reference listing of species and specimens used in the private collection of LWP..

DESCRIPTION (Male). Figs 1, 36A. *Head.* Sandy brown to pale brown and black. Supra-antennal plate, gena and mandibular plate dominantly black, with small pale brown spot between ocelli, extending to posterior margin; small pale brown spots along anterior margin of supra-antennal plate extending around base of antennae. Ocelli pink to pale red. Compound eyes brown to dark brown. Postclypeus with pale brown margin; remainder, including transverse ridges, black. Anteclypeus black. Rostrum dark brown, black proximally. Antennae uniform medium brown.

*Thorax.* Sandy brown, brown and black. Pronotum sandy brown with paler central fascia enclosed by narrow black rim which flares out adjacent to anterior pronotal margin and adjacent to pronotal collar; broken to diffuse black to dark brown areas between the anterior and posterior oblique fissures and between posterior oblique fissure and pronotal collar; pronotal collar pale sandy brown, grading to black at lateral corner; moderately ampliate along lateral margin. Mesonotum with a pair of anterior broad obeonical fasciae fused dorsally and extending less than half the length to the cruciform elevation; two very broad lateral fasciae, narrowing towards and just reaching the proximal arms of cruciform elevation; remainder, including cruciform elevation, pale sandy brown with diffuse darker colouration between arms of cruciform elevation; wing grooves pale sandy brown with silver pubescence.

*Wings.* Fore wing venation pale brown grading to medium brown distally. Costal vein pale sandy-brown to translucent; weakly developed node on costal vein; basal membrane pale pink-brown; dark brown pterostigma. Hind wing plaga opaque white, extending along vein 3A.

*Legs.* Glossy. Fore coxae pale sandy brown, partially black on anterior and medial inner faces; mid and hind coxae dominantly black on anterior and lateral faces, pale sandy brown along ventral margins. Trochanters and lateral faces of fore femora pale sandy brown, with three black spines; inner faces of femora dominantly dark brown to black. Mid and hind femora pale sandy brown with broad medium to dark brown anterior and lateral margins. Tibiae and tarsi pale sandy brown; claws sandy brown, with dark brown apices.

*Operculae.* Pale brown, with dark brown patches within basal parts (especially anteriorly), and also proximal to crest around distolateral areas; meracantha elongated to a relatively acute point; distal margin does not extend distally to anterior paramedial margin of sternite II.

*Timbals.* Ribs 1-4 extensively fused ventrally; a remnant small anterior rib (5).

*Abdomen.* Tergites brown to reddish-brown with well defined median black areas, each tapering distally, giving the overall appearance of a longitudinal black dorsal fascia; sporadic lateral patches of pale brown colour on tergites 3 (most common)-4 (± 5); auditory capsules black with dark brown central areas, the black extending to adjacent area and along anterior margin to tergite 2; fine silver pubescence paramedially and laterally; posterior margins of tergites and intersegmental membranes yellow. Sternites pale to medium reddish brown, darker distally; medium brown on sternite VII and VIII; small black blotch ventro-medially on sternite II.

*Genitalia.* Pygofer medium to dark brown. Upper lobe relatively acutely terminated. Otherwise as in generic characters.

FEMALE. Fig. 36B. Generally similar to male. Supra-antennal plate, gena and mandibular plate black, with pale colouration as in male. Postclypeus with broader outer pale brown margin, transverse ridges black to deep brown. Pronotum dominantly pale sandy brown with thinner dark margin enclosing central fascia. Mesonotum and legs as in male. Tergite colouration, including black dorsal markings as in male. Tergite 9 sandy brown with dark brown paramedial fasciae extending more than three-quarters of the distance to distal margin and also ventro-laterally along anterior margin. Ovipositor sheath extends ≤0.5 mm beyond tergite 9 termination. Sternites uniformly pale sandy brown.

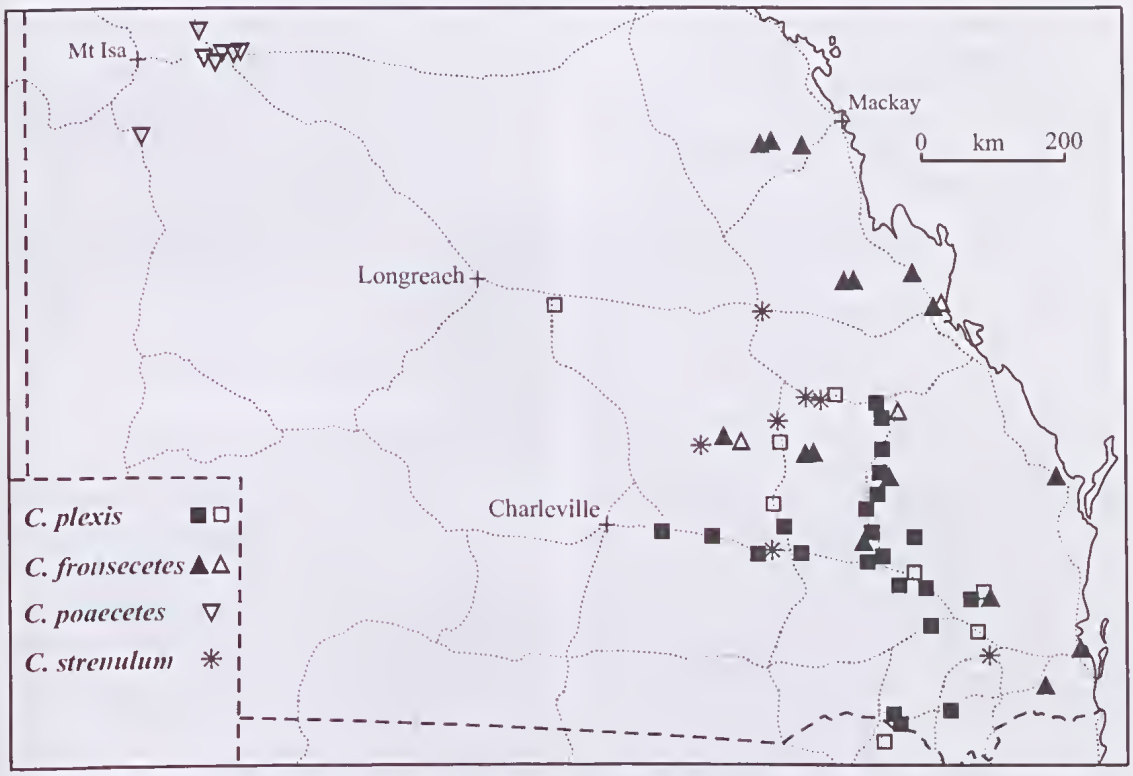


FIG. 2. Distribution records of the four *Crotopsalta* ticking cicadas described, in Queensland and northeastern N.S.W. Data include aural records, indicated by hollow symbols for *C. plexis* and *C. fronsecetes*.

MEASUREMENTS. N = 10♂, 10♀. Ranges and means (in parentheses). *BL*: ♂ 9.7-10.8 (10.2); ♀ 10.8-12.2 (11.7). *FWL*: ♂ 11.2-12.4 (11.7); ♀ 12.4-13.5 (13.2). *HW*: ♂ 2.9-3.4 (3.2); ♀ 3.4-3.6 (3.5). *PW*: ♂ 2.6-3.1 (2.9); ♀ 3.0-3.5 (3.5). *AW*: ♂ 2.8-3.1 (3.0); ♀ 3.0-3.4 (3.2). *FWL/BR*: ♂ 2.53-2.86 (2.72); ♀ 2.60-2.84 (2.73).

DISTRIBUTION, HABITAT & BEHAVIOUR (Fig. 2). Occurs widely through inland southern and central Queensland, from the dividing range west to the Morven and Barcaldine regions. A single aural record exists from near North Star, NNW of Warialda, NSW. Restricted to mixed and disturbed brigalow (*Acacia harpophylla*) - wilga (*Geijera parviflora*) - belah (*Casuarina cristata*) - limebush (*Eremocitrus glauca*) - scrub boonaree (*Heterodendrum diversifolium*) - false sandalwood (*Eremophila mitchelli*) - vegetation communities, and less commonly in Poplar Box (*Eucalyptus populnea*) and silver leaved ironbark (*E. melanophloia*) woodlands. This species has particularly strong affinities with wilga and *E. mitchellii*. It is highly cryptic and mobile, flying quickly and unobtrusively for ≥40 m, although usually much shorter distances. It inhabits outer foliage of shrubs and trees, usually where foliage is dense. Small size, colour, and rapid flight make it a very difficult insect to see. The ticking song is emitted incessantly during the day, even during light rain. Where multiple insects occur in the same tree or shrub, ticking may occur in unison, although sometimes fractionally offset. It occurs from late August/ September to February, based on collected material and aural records.

SONG. (Figs 7-11; Table 2). A soft slow ticking with pulse repetition rate in the range 1.0-3.2 per second. This song is a distinctive field identification character. Further technical and comparative details of the songs follow the taxonomic descriptions of *Crotopsalta species*.

ETYMOLOGY. Greek *plexi(s)*, stroke or sharp percussion; refers to the slow sharp ticking song.

COMPARISON. This species is superficially similar to *Pauropsalta stigmatica* Distant.

**Crotopsalta fronsecetes** sp. nov.
(Figs 2, 3, 4, 7-11, 37, Table 2)

*Notopsalta* sp. J: Ewart, 1998: 65, figs 10B, C, 13C.

MATERIAL. HOLOTYPE; ♂, QMT99210, Meadowlands Rec. Reserve, Carina/Belmont, Brisbane, Q., 9543/116587, 23.xii.1997.

PARATYPES: SOUTH AND CENTRAL QUEENSLAND: 3♂, 1♀, ~4 km N. from Glendon-Peak Downs Hwy Rd jet, AE, 22.x.2000, 21°37.27'S 148°39.47'E; 1♂, As previously, Rec spec 1; 1♂, As previously, Rec spec 2; 1♂, ~8 km SW Homevale HS, Homevale NP, AE, 23.x.2000, 21°28.67'S 148°27.69'E; 1♂, ~9 km SW Homevale HS, Homevale NP, AE, 23.x.2000, 21°29.48'S 148°27.25'E; 1♂, ~7.5 km WSW Homevale HS, Homevale NP, AE, 23.x.2000, 21°28.01'S 148°27.58'E; 2♂, 1♀, 25°12'S 148°59'E, Expedition Ra NP, 'Amphitheatre' camp, 560m, 17.xii.1997, SE, CB, AE, Mv lamp, open forest; 13♂, 8♀, The Amphitheatre, NW Robinson Gorge N.P., 25°12.07'S 148°59.43'E, Open Forest, 17.xii.1997, AE, CB, SE; 3♂, Fitzroy R xing, 68 km NW Rockhampton, 10.x.1999, AE, 23°10.81'S 149°55.08'E; 1♂, As previously, Rec (spec 1); 1♂, As previously, Rec (spec 2); 1♂, Boomer Ra NP, NW Rockhampton, AE, CB, GBM, SE, 30.ix.1999, 23°12.88'S 149°44.37'E, Rec; 1♂, Amphitheatre, Expedition Range NP, 560m., 18.xii.1997, 25°12'.S 148°59'E, AE, Rec box; 2♂, 41km SE Childers, Bruce Hwy, 30.x.2001, AE, 25°23.22'S 152°36.03'E; 1♂, As previously, Rec spec 1; 1♂, As previously, Rec spec 2; 2♀, 9.0 km NW Yaamba, Bruee Hwy., 8.xi.2001, AE, light, 23°06.22'S 150°17.49'E; 1♂, As previously, Rec spec 1; 1♂, As previously, Rec spec 2; 16♂, 2♀, Gurulmundi, Miles, heath, 26°25.20'S 149°59.50'E, 9.x.1997, AE; 1♂, As previously, Rec; 1♂, Gurulmundi, Miles, heath, 26°25.20'S 149°59.50'E, 25.ix.1997, AE; 5♂, 1♀, Gurulmundi heath, N. of Miles, 22.xi.1997, 26°25.20'S 149°59.50'E, AE; 16♂, 4♀, Meadowlands Reserve, Carina/Belmont, Brisbane, 9543/116587, 23.xii.1997: 1♂, As previously, Rec; 1♂, Gurulmundi heath, N. Miles, 17.x.1998, 26°25.13'S 149°59.48'E, AE; 2♂, As previously, Rec; 1♂, 1♀, 7.2 km N.E. Maclagan, 19.i.2004, AE, 27°03.13'S 151°41.64'E, In Cop; Ree (male) **(AE)**. 3♂, Meadowlands Park, Carindale, 11.xi.2000, LWP, 351-0021, 0022; 11♂, 1♀, Meadowlands Park, Carindale, 22.xi.1998, LW&RP, 351-0003 to 351-0014; 5♂, Meadowlands Park, Carindale, 24.x.1998, LW&RP, 351-0016 to 351-0020; 4♂, 1♀ Meadowlands Park, Carindale, 16.x.2001, LWP, 351-0024 to 351-0028; 5♂, 1♀, Minto Crags (south faee), S Boonah, 3.xi.2001, LWP, JM, RS, 351-0030 to 0036: 1♂, Minto Crags (south face), S. Boonah, 3.xi.2001, LWP, JM, RS, minidise (LWP); 4♂, Gurulmundi SF, 28 km N. Miles, 2-3.xii.1999, JM, LWP, 355-0001 to 0004; 1♂ Meadowlands Park, 6.xii.1998, LWP, *ex Casuarina glauca* 351-0029; 1♂, Meadowlands Park, Carindale, Brisbane, 23.xii.1997, LWP, *Casuarina glauca*, Rec, 351-0015 **(LWP)**. 1♀, 25°26'Sx150°01'E, Boggomoss No. 3, via Taroom, 12.xi.1996-i.1997, DC, GBM, Baited Flight Intercept 041; 1♂, 25°01'S 147°57'E, Rangers HQ, Mt. Moffat NP, 2.xii.1997, SE, CL, JS, mv lamp; 14♂, 11♀, 25°12'S 148°59'E, 'Amphitheatre' campsite, Expedition Ra NP, 560m, 17.xii.1997, CB, SE, AE, mv lamp, open forest; 11♂, 15♀, 24°54' 148°59'E, Expedition Ra NP, 'Amphitheatre' camp, 560 m, 18.xii.1997, AE, CB, SE, mv lamp, open forest; 1♀, 23°12'Sx149°64'E, Boomer Ra, Mongrel Scrub Site 7, vine scrub, 220 m., 16.xii.1999-2.iii.2000, GBM, intercept 9119 **(QM)**. 1♂, Rockhampton, 5.i.1968, FRW **(UQIC)**. 1♂, 1♀, The Amphitheatre, NW Robinson Gorge NP, 25°12.07'S 148°59.43'E, open forest, 17.xii.1997, AE, CB, SE, **(BMNH)**. 1♂, 1♀, The Amphitheatre, NW Robinson Gorge NP, 25°12.07'S 148°59.43'E, open forest, 17.xii.1997, AE, CB, SE, **(ANIC)**. 1♂, 1♀, The Amphitheatre, NW Robinson Gorge NP, 25°12.07'S 148°59.43'E, open forest, 17.xii.1997, AE, CB, SE, **(MSM)**.

DESCRIPTION (Male). Figs 3, 4, 37A. *Head.* Black and pale brown. Supra-antennal plate black with small lanceolate pale to yellow brown area between ocelli, pointing anteriorly, and extending to posterior plate margin; pale brown zone enclosing bases of antennae along anterior rim of plate (not always present). Ocelli red. Compound eyes dark brown. Postclypeus black with pale brown anterior margin. Gena and mandibular plate black with silver pubescence. Anteclypeus black, in some specimens grading pale brown distally. Rostrum dark brown, darker apically. Antennae dark brown.

*Thorax.* Black to brown. Pronotum with narrow central fascia pale brown enclosed by broad black envelope which flares outwards adjacent to both anterior and posterior pronotal margins; broken black areas between anterior and posterior oblique fissures, and also along and lateral to the posterior oblique fissures; remaining colour medium brown; pronotal collar black anteriorly and at corners, otherwise pale brown; markedly ampliate along lateral margins. Mesonotum with a pair of anterior broad paramedian obconical areas coalescing medially and extending longitudinally to near the cruciform elevation; a pair of broad lateral fasciae tapering distally and extending to, and partially enclosing, the outer arms of the cruciform elevation; cruciform elevation and mesonotum pale to medium brown; arms of cruciform elevation black in some specimens; wing grooves pale brown rimmed by silver pubescence.

*Wings.* Fore wing venation pale to medium brown, darker distally; pale sandy brown to translucent costal vein; venation proximal to basal cell pale yellow brown; pterostigma deep reddish-brown to dark brown; weakly developed costal node; basal membrane sandy brown. Hind

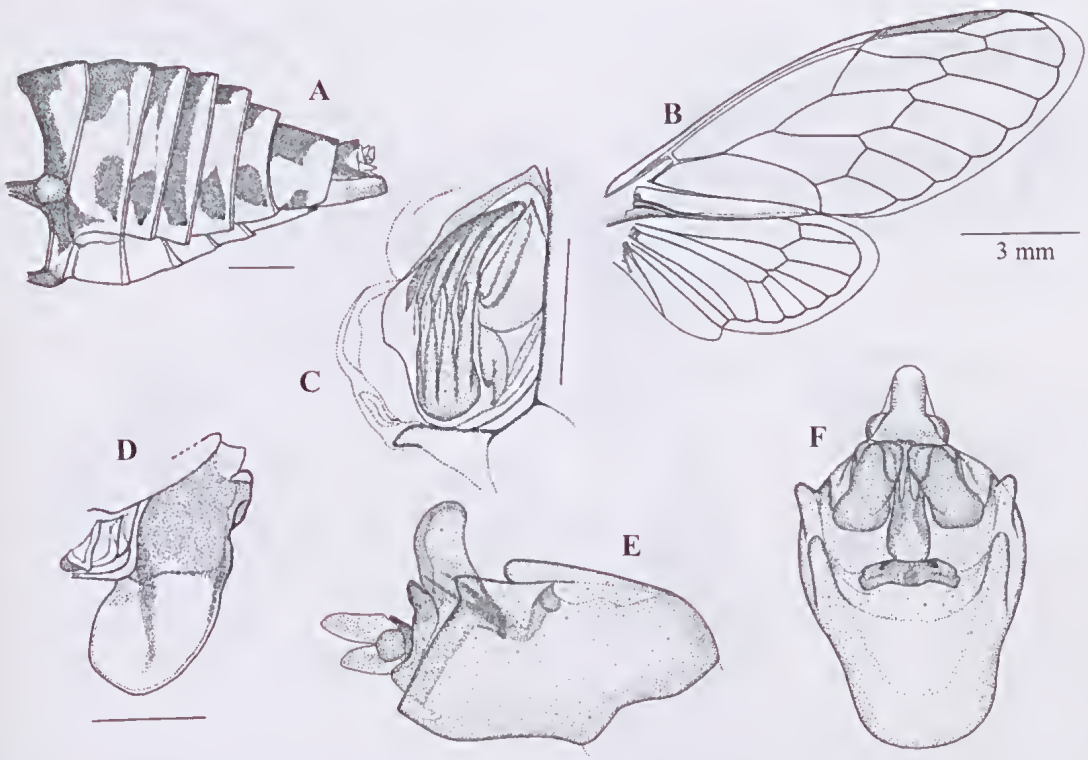


FIG. 3. *Crotopsalta fronsecetes*. A, Lateral abdomen view; B, fore and hind wings; C, timbal; the right-hand edge as shown represents the posterior margin, the top the dorsal edge; D, opereula; E, and F, lateral and ventral views of pygofer. Length of pygofer 1.6mm. Scale bars = 1 mm except wings (3mm). Drawings from specimens from the Expedition Range National Park.

wing venation medium to dark brown; plaga opaque off-white colour extending narrowly along the margin of the 3A vein.

*Legs*. Fore coxae pale brown with extensive deep to medium brown areas on anterior and lateral surfaces; mid and hind coxae black to dark brown on anterio-lateral faces; pale brown on inner (medial) faces. Fore femora and trochanters black to deep brown on anterior faces, with dark to medium brown and pale brown diffuse longitudinal fascia on lateral faces; mid and hind femora and trochanters pale brown with darker brown longitudinal fasciae. Tibiae dark to pale brown, paler on mid to hind legs. Tarsi pale brown, darker distally, with dark brown claws.

*Operculae*. Rounded distal margins; pale yellow brown between the distal areas to transverse sutures; basal parts varies from mostly brown to black, to only darkly coloured along lateral margins; localised pale brown at crest around dorsolateral basal corners; meracantha yellow-brown, elongated with acute termination apically, extending over medial areas; distal margins of opercula extend to anterior paramedial margin of sternite II.

*Timbals*. Although ribs 1-3 are always fused ventrally, rib 4 is variable in some specimens; it is either fused or weakly fused to ribs 1-3 (most common), or is not fused to ribs 1-3; it also may be either continuous across timbal or discontinuous in the thinned median region; the anterior rib 5 is also variable in different specimens, varying from a small remnant to a shortened rib extending to median area; three to four short ribs are present, sometimes thin and poorly defined.

*Abdomen*. Tergites pale brown to reddish brown, usually grading darker in colour on tergites 5-7; each tergite has a black dorsal area, each of which narrows towards posterior margin and becomes progressively smaller towards tergite 7; this

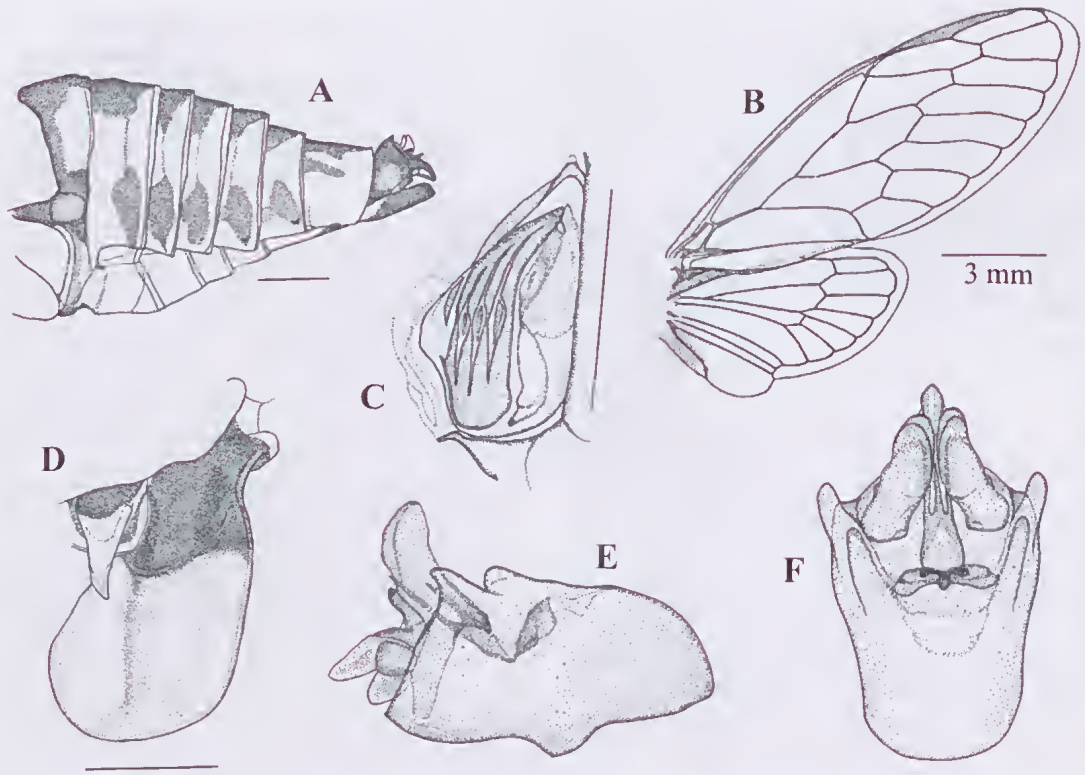


FIG. 4. *Crotopsalta fronsecetes* with slower than normal ticking rate. A, Lateral abdomen view; B, fore and hind wings; C, timbal; the right-hand edge as shown represents the posterior margin, the top the dorsal edge; D, opereula; E, and F, lateral and ventral views of pygofer. Length of pygofer 1.6mm. Scale bars = 1mm except wings (3mm). Drawings from specimens from heath at Gurulmundi, north of Miles.

pattering gives the overall appearance of a black fascia extending dorsally along abdomen; black colouration on tergite 2 extends laterally along anterior margin towards and including the auditory capsules, this being dark brown centrally; tergites 3-6 (±7) have well defined, but relatively localised black areas of colouration developed laterally; distal margins of each tergite, including intersegmental membranes, yellow-brown to pale brown. Sternite II medium to dark brown, black in ventro-medial area; sternites III-VII uniformly pale to medium brown, darker distally; sternite VIII medium to dark brown.

*Genitalia*. Pygofer colour dark brown grading to black distally. Other details as in generic characters.

FEMALE. Fig. 37B. Head similar to male. Postelypeus with more extensive pale brown colouration and dark brown transverse ridges. Pronotum and pronotal collar similar to male but with black colouration reduced in extent. Mesonotum similar to male, but with broad black fasciae reduced in width, and greater area of brown colouration, including cruciform elevation. Wings as in male, fore wing basal membrane and hind wing plaga pale pinkish-brown. Legs similar to male. Abdomen similar to male, but with generally reduced darker colouration dorso-laterally. The tergite dorsal black areas, in some specimens, continue as thinned streaks dorso-laterally and coalesce with the darker lateral areas; black anterior colouration on tergite 2 is discontinuous paramedially; distal tergite margins pale yellow-brown to brown; tergite 8 with a pair of bluntly terminated paramedial, slightly curved black fasciae, extending approximately three-quarters along the length of the tergite, the dark colouration also extending dorsolaterally along the anterior margin of tergite. Sternites II-

VI pale sandy brown; sternite VII with small black discontinuous area adjacent to distal edge. Ovipositor sheath extends ≤0.5mm beyond tergite 9.

MEASUREMENTS. N=11♂, 10♀. *BL*:♂ 9.1-11.9 (11.0); ♀ 11.2-12.4 (11.7). *FWL*: ♂ 10.7-13.2 (12.4); ♀ 12.7-13.5 (13.1). *HW*: ♂ 2.8-3.6 (3.3); ♀ 3.2-3.7 (3.4). *PW*: ♂ 2.5-3.2 (3.1); ♀ 2.9-3.4 (3.2). *AW* ♂ 2.6-3.3 (3.1); ♀ 2.8-3.6 (3.2). *FWL/BR*: ♂ 2.63-3.04 (2.83); ♀ 2.66-2.88 (2.78).

DISTRIBUTION, HABITAT & BEHAVIOUR (Fig. 2). Occurs widely through Queensland from Mt. Maroon area in the southeastern corner, through Brisbane, northwards including areas north of Maryborough, Emu Park (aural record, east of Rockhampton) to the Homevale National Park region (southwest of Mackay). Inland distributions extend from north of Miles to the Expedition Range National Park (southeast of Rolleston) and the Mt. Moffat and Carnvarvon National Parks (latter an aural record). It appears to be a localised species, but common to abundant where present. It occurs dominantly in eucalypt woodland, including narrow-leaved ironbark (*Eucalyptus crebra*); silver-leaved ironbark (*E. melanophloia* ) and mountain coolibah (*E. orgadophila* ) and associated lower tree layers, especially acacias (e.g. *A. concurrens*). It is also found in open casuarina woodland (e.g. *C. cristata* ), less commonly in surrounding long grass and shrubs (e.g. wild cottonbush, *Gomphocarpus physocarpus*, in disturbed areas), and isolated areas of False Sandlewood (*Eremophila mitchellii*). A distinctive and apparently atypical localised occurrence is in heath near Gurulmundi (north of Miles) where this species occurs abundantly in *Kunzea opposita* and *Melaleuca uncinata*. This occurrence is of further interest as the ticking song is slightly slower than normal (see below). *C. fronsecetes* is highly cryptic, small, very wary and fast flying. It most often inhabits branches within tree foliage, moving frequently between branches and also readily between trees. In warm weather, the rapid ticking song is emitted incessantly from morning to late afternoon. In cooler weather, singing occurs between late morning and mid afternoon. Occurs September-January, most abundant in December.

SONG (Figs 7-11; Table 2). A soft rapid ticking with pulse repetition rate between 5.0-11.5 per second. This is intermediate between *C. plexis* and *C. strenulum* (Fig. 11). The population from the Gurulmundi heath location is notable for its consistently slower pulse repetition rate than observed elsewhere, the respective means and standard deviations (field recordings) being 5.9±0.6 compared to 8.1±1.5 for all data. The individually measured pulse rates do, however, overlap and in view of their close morphological and colour similarities (Figs 3, 4) and the similarity of pulse structures (Fig. 8), there is no justification for defining the Gurulmundi population as a separate species or subspecies.

ETYMOLOGY. Latin *frons* and Greek *ecetes*, meaning foliage dweller.

**Crotopsalta strenulum** sp. nov.
(Figs 2, 5, 7-11, 38, Table 2)

MATERIAL. HOLOTYPE; ♂, QMT99211, Nogoa R. xing, Emerald, C.Q., Ewart, 25 Oct 2000, 23°31.95'S 148°10.12'E.

PARATYPES: SOUTH AND CENTRAL QUEENSLAND: 3♂, Nogoa R xing, Emerald, AE, 25.x.2000, 23°31.95'S 148°10.12'E; 1♂, As previously, Field Rec; 1♂, As previously, Rec spec 1; 1♂, As previously, Rec spec 2; 16♂, 3.3 km E. of summit Expedition Ra, AE, 26.x.2000, 24°39.13'S 149°02.57'E; 1♂, As previously, Rec spec 1; 1♂, As previously, Rec spec 2; 1♂, As previously, Rec spec 3; 1♂, 5.6 km W. Summit Expedition Ra, (36 km W. Bauhinia), Hwy, 13.ii.1999, AE, grass, 24°37.03'S 148°54.83'E, Rec; 16♂, 16km E Muckadilla, grassland, 16.xii.2000, AE, 26°34.95'S 148°32.74'E; 1♂, As previously, Rec spec 1; 1♂, As previously, Rec spec 2; 12♂, 1 exuviae, Nogoa R, E side Emerald, grass, open shrubland, 14.xii.2000, AE, IR, 23°31.95'S 148°10.16'E; 2♂, 5.7 km W Expedition Ra summit, Rolleston Rd, grass, AE, 29.xii.2002, 24°36.70'S 148°58.46'E; 1♂, As previously, Rec; 2♀, Nogoa R, E side Emerald, grass, open shrubland, 13.xii.2000, AE, IR, 23°31.95'S 148°10.16'E; 8♂, Wyseby-Carnarvon Rd jct, 200m W, CQ, grass, AE, 15.xii.2004. 23°58.24'S 148°31.49'E; 1♂, As previously, Rec; 1♂, 1.2km W Wyseby-Carnarvon Rd jct, CQ, grass, AE, 18.xii.2004, 24°58.39'S 148°31.06'E; 1♂, 3.4km W Wyseby-Carnarvon Rd jct, CQ,, grass, AE, 18.xii.2004, 24°59.00'S 148°29.97'E **(AE)**. 9♂, 4♀, Westbrock Ck, 7 km W Drayton, 29.xi.2001, LWP, JM, 353-0001 to -0004; 1♂, Westbrook Ck, 7 km W Drayton, 29.xi.2001, LWP; 1♂, 24°54'51"S 148°01'31"E, Rotary Shed, Mt Moffat NP, 16.i.2005, LWP, 353-0015 **(LWP)**. 1♂, 25°08.22'S 147°30.37'E, Mt. Moffat NP, W. Branch Maranoa R, 21.xi.1995, 660m Irwin, Gaimari, DY, CB, malaise **(QM)**. 1♂, Nogoa R, E side Emerald, grass, open shrubland, 13.xii.2000, AE, IR, 23°31.95'S 148°10.16'E **(BMNH)**. 1♂, Nogoa R, E side Emerald, grass, open shrubland, 14.xii.2000, AE, IR, 23°31.95'S 148°10.16'E **(ANIC)**. 1♂, Nogoa R, E side Emerald, grass, open shrubland, 13.xii.2000, AE, IR, 23°31.95'S 148°10.16'E **(MSM)**.

DESCRIPTION (Male). Figs 5, 38A. *Head*. Sandy brown and black. Supra-antennal plate

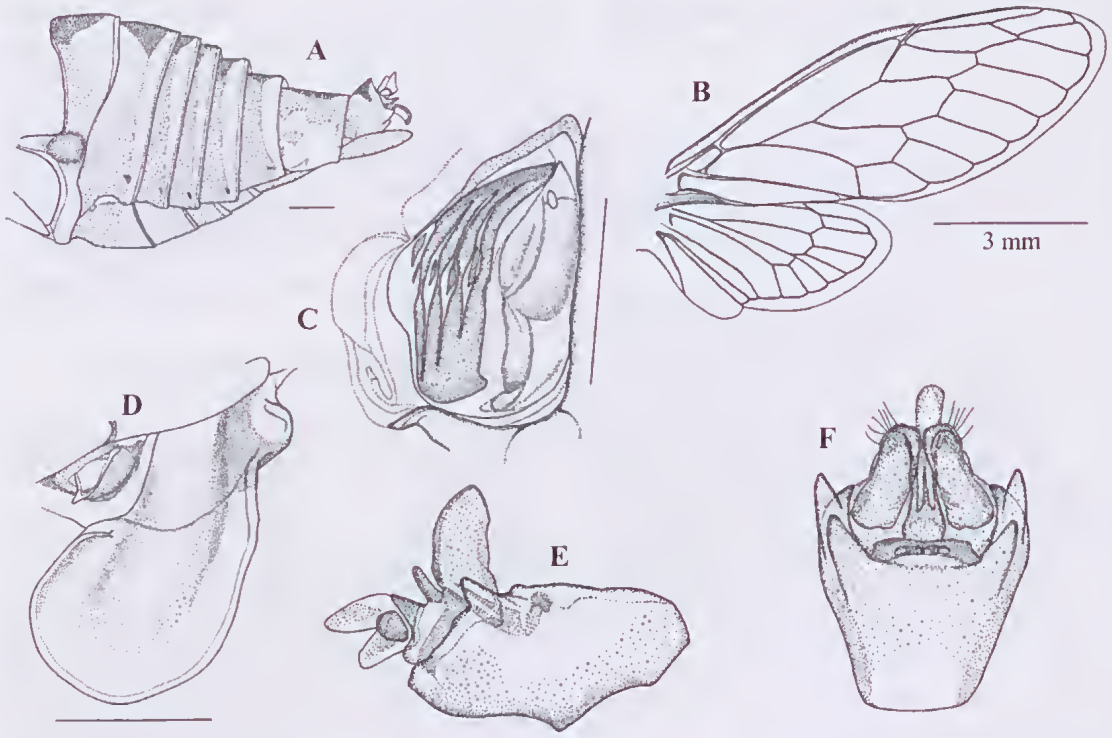


FIG. 5. *Crotopsalta strenulum*. A, Lateral abdomen view; B, fore and hind wings; C, timbal; the right-hand edge as shown represents the posterior margin, the top the dorsal edge; D, opercula; E, and F, lateral and ventral views of pygofer. Pygofer length 1.4mm. Scale bars = 1mm except wings (3mm). Drawings based on specimens from near the summit of the Expedition Range, west of Bauhinia, and Nogoa River at Emerald (abdomen only).

black with small yellow-brown area between ocelli, extending to distal margin; a pair of localised small sandy brown areas enclosing bases of antennae. Postclypeus pale brown with transverse ridges and central area black. Gena and mandibular plate black. Ocelli red. Compound eyes dark brown. Anteclypeus dark brown to black. Rostrum pale brown, darker apically. Antennae dark brown.

*Thorax*. Sandy brown and black. Pronotum dominantly sandy brown; central fascia yellow-brown enclosed by narrow black envelope which flares outwards along the anterior and especially posterior pronotal margins; small broken irregular black areas between anterior and posterior oblique fissures, and dark brown colouration extending along posterior oblique fissure; pronotal collar yellow- brown, darker at lateral corners; markedly ampliate along lateral margins. Mesonotum sandy brown with a pair of anterior broad, but short black obconical fasciae which coalesce near anterior margin of mesonotum and which extend distally about half way to cruciform elevation; a pair of black broad lateral fasciae tapering distally, extending to anterior arms of cruciform elevation; cruciform elevation pale sandy brown, with diffuse darker brown colouration between anterior arms; wing grooves pale sandy brown with silver pubescence along margins.

*Wings*. Fore wing venation pale to medium brown, darkening apically; costal vein pale sandy brown to translucent; weakly developed node; pterostigma dark reddish-brown; basal membrane pale brown. Hind wing venation brown, darkening apically; plaga opaque white, extending partially along vein 3A.

*Legs*. Coxae pale sandy brown, with broad dark brown anterior longitudinal fasciae. Trochanters and femora sandy brown, with variable darker brown longitudinal fasciae along anterio-dorsal edges, broader on fore femora. Tibiae and tarsi pale brown to pale sandy brown, darker on

TABLE 2. Comparative song parameters of the four *Crotopsalta* ticking cicadas. [1] Pulse doublets counted as 1 pulse; [2]Container data only; [3]Specifically the frequency of dominant spectral peaks.

| | *C.plexis* | *C.fronsecetes* | *C.strenulum* | *C.poaecetes* |
|---|---|---|---|---|
| **I Tick repetition rates ($s^{-1}$,±σ)** | | | | |
| - Container recordings | 1.81±0.50 (n=52) | 7.42±1.36 (n=40) | 10.04±1.08 (n=34) | 4.43±0.90[1,2] (n=23) |
| - Field recordings (open sunlight) | 2.75±0.15 (n=3) | 8.14±1.85 (n=25) | 15.74±2.97 (n=6) | - |
| Field (Container) recordings | | | | |
| - Minimum | 2.7(1.0) | 5.0(5.0) | 11.7(7.4) | (3.5)[1,2] |
| - Maximum | 2.9 (3.2) | 11.5(9.5) | 20.4(12.4) | (6.9)[1,2] |
| **II Pulse lengths and separations (ms,±1σ)** | | | | |
| (a) *First and second pulses clearly separate:* | | | | |
| First pulse | 8.1±1.3 (n=29) | 8.6±1.7 (n=22) | 7.8±0.5 (n=6) | 7.9±1.0 (n=17) |
| Second pulse | 5.1±1.2 | 3.9±1.0 | 3.8±0.9 | - |
| Inter-pulse duration | 18.4±5.3 | 13.5±3.0 | 10.2±1.1 | 32.6±4.2 |
| | | | | |
| (b) *First and second pulses without clear separation:* | | | | |
| First pulse | - | - | 9.7±1.6 (n=15) | - |
| Second pulse | - | - | 4.5±1.0 | - |
| (c) *Second and third pulses coalesced into single pulse:* | - | - | | 7.5±0.7 (n=6) |
| (d)*Second and third pulses well defined but without separation:* | | | | |
| Second pulse | - | - | - | 3.5±1.3 (n=7) |
| Third pulse | - | - | - | 6.7±1.0 |
| Total length of pulse 2 + pulse 3 | - | - | - | 10.2±1.4 |
| (e) *Pulse 2 and 3 clearly separated:* | | | | |
| Pulse 2 | - | - | - | 4.5±0.3 (n=3) |
| Pulse 3 | - | - | - | 5.2±0.6 |
| Total length pulse 2 + pulse 3 | - | - | - | 9.7±0.9 |
| **III Maximum Frequeney (kHz)[3]** | 14.7(n=34) | 14.8(n=21) | 14.9(n=27) | 14.9(n=15) |
| **Mean Frequency (kHz)** | 13.1 | 13.2 | 13.9 | 13.7 |

forelegs. Claws pale brown, with dark brown tips.

*Operculae.* Elongated, but with slightly expanded and rounded at distal-medial margins; colour pale yellow-brown; in some specimens, localised darkening of colour occurs adjacent to distolateral crest, on basal areas, and very localised darkening on medial areas of cross suture; meracantha relatively acutely terminated; distal margins extend distally to anterior paramedial margin of sternite II.

*Timbals.* Ribs 1-4 fused ventrally; rib 4 continuous across timbal, rib 5 shortened; 5short ribs.

*Abdomen.* Tergites 2 and 3 pale sandy brown, grading to medium brown on tergites 4-8; black areas present dorsally on each tergite, each narrowing distally, giving the overall appearance of a continuous black dorsal fascia extending the length of the abdomen; tergite 2 additionally possesses a thin, discontinuous black anterior margin in some specimens; tergites 3-7 with localised medium to dark brown irregular lateral patches; auditory capsules centrally yellow brown with diffuse, thin black to dark brown margins. Sternites II and III yellow-brown, grading to chestnut brown in sternites IV-VII;

sternite II with a small medium black patch near posterior margin; sternite VIII medium brown.

*Genitalia*. Pygofer medium to dark brown. Upper lobe extended into small, acutely rounded shape. Other details as in generic description.

FEMALE. Fig. 38B. *Head*: Supra-antennal plate dark brown to black with anterior-pointing triangular yellow-brown spot between ocelli, and small pale areas enclosing bases of antennae. Postclypeus sandy brown with dark brown transverse ridge and central area. Pronotum with pale yellow-brown central fascia enclosed by thin darker brown envelope which only slightly flares outwards along the anterior and posterior pronotal margins; remaining pronotum sandy brown with thin curved slightly darker brown dorso-lateral fascia. Mesonotum sandy brown with a pair of short broad paramedial obconical black fasciae, broken by veinlets of pale colouration, and almost or very weakly fused anteriorly; a pair of broad lateral fasciae extending to anterior arms of cruciform elevation, as in male, but broken by veinlets and lobes of pale brown colouration. Legs similar to male, but generally paler. Abdomen; tergites variably coloured pale to medium brown, with dorsal black areas absent (as seen in male), although local darker brown lateral areas present on tergites 3-5; overall colour of tergites are paler than in male; tergite 9 with pale to medium brown paramedial fasciae extending distally approximately three-quarters of the length of tergite. Sternites uniformly sandy brown. Ovipositor sheath extends ≤1mm beyond tergite 9.

MEASUREMENTS. N = 10♂, 6♀. *BL*: ♂ 8.6-10.4 (9.8); ♀ 10.3-11.9 (11.0). *FWL*: ♂ 10.0-11.4 (10.7); ♀ 11.8-12.1 (11.9). *HW*: ♂ 2.7-3.0 (2.8); ♀ 3.0-3.3 (3.1). *PW*: ♂ 2.5-3.0 (2.7); ♀ 2.8-3.0 (2.9). *AW*: ♂ 2.5-3.1 (2.9); ♀ 3.1-3.4 (3.2). *FWL/BR*: ♂ 2.39-2.72 (2.57); ♀ 2.42-2.58 (2.51).

DISTRIBUTION, HABITAT & BEHAVIOUR (Fig. 2). A very small cicada occurring in open grassland and grassland within open woodland. It is a very cryptic, fast flying and wary species, constantly moving (up to ~5m) when singing. In between singing phases, it will sit quietly on grass stems. Distributed southeastwards from Emerald to over the Expedition Range between Rolleston and Bauhinia. Other occurrences in southern Queensland include the Mt. Moffat National Park; Wyseby; 25km W of Roma (in mitchell grassland); and 7 km west of Drayton. The populations are usually extremely common, but very localised, typically limited to areas less than approximately 300m diameter. An exception was located near Wyseby where the cicada occurred continuously in grassland along the Carnarvon National Park road for 3.4km. A preference for clay-rich alluvial and basalt soils is suggested by available data. Available records are during October to February.

SONG (Figs 7-11; Table 2). An extremely rapid ticking, the fastest of the four *Crotopsalta* species described, providing a diagnostic field criterion. The pulse repetition rate lies in the range 7.4-20.4 per second.

ETYMOLOGY. Latin *strenu*, active and diminutive suffix *-ulum*; referring to its small size and active behaviour.

**Crotopsalta poaecetes** sp. nov.
(Figs 2, 6, 7-11, 39, Table 2)

MATERIAL. HOLOTYPE; ♂, QMT99212, Cloncurry, E. side, NWQ., 3 Feb 1999, AE., 20°43.27'S 140°31.32'E, Recorded.

PARATYPES: NORTHWESTERN QUEENSLAND: 4♂, 2♀, Cloncurry, E side, 3.ii.1999, AE, 20°43.27'S 140°31.32'E; 9♂, 1♀, 11 km E Cloncurry Hwy, 4.ii.1999, AE, 20°43.41'S 140°37.47'E; 1♂, Cloncurry R bridge, 1.2 km W. Cloncurry, 4.ii.1999, AE, 20°42.24'S 140°29.88'E; 6♂,~2 km SE Cloncurry, grass, AE, 23.i.2000, 20°43.52'S 140°31.10'E; 5♂, 4♀, ~2 km SE Cloncurry, grass, AE, 25.i.2000, 20°43.52'S 140°31.10'E; 1♂, As previously, Rec; 2♂, 2♀, ~2 km SE Cloncurry, grass, AE, 24.i.2000, 20°43.52'S 140°31.10'E; 1♂, As previously, Rec; 2♂, 29 km W Cloncurry, grass, AE, 24.i.2002, 20°44.27'S 140°15.01'E; 1♂, As previously, Rec, 1♂, Quamby, 44 km N. Cloncurry, AE, grass and forbs, 25.i.2002, 20°22.48'S 140°17.19'E, Rec; 1♂; Dajarra township, grass, AE, 20.i.2002, 21°41.76'S 139°31.05'E, Rec spec 1; 1♂, As previously, Rec spec 2; 2♂, 34 km E Cloncurry, grass, AE, 26.i.2002, 20°41.59'S 140°48.86'E; 1♂, As previously, Rec **(AE)**. 1♂, 29 km W Cloncurry, grass, AE, 24.i.2002, 20°44.27'S 140°15.01'E **(BMNH)**. 1♂, 34 km E Cloncurry, grass, AE, 26.i.2002, 20°41.59'S 140°48.86'E **(ANIC)**. 1♂, ~2 km SE Cloncurry, grass, AE, 25.i.2000, 20°43.52'S 140°31.10'E **(MSM)**.

DESCRIPTION (Male). Figs 6, 39A. *Head*. Pale sandy brown and black. Supra-antennal plate partially black, with the following: a pair of lozenge-shaped pale sandy brown areas, joined adjacent to the distal margin of head, and splaying outwards anteriorly, thereby partially enclosing the two posterior ocelli and terminating adjacent to, but not enclosing, the anterior ocelli; a pair of inward pointing pale sandy brown to brown areas adjacent to inner margins of compound eyes; a small pale area between the anterior ocelli and postclypeus; sandy brown colouration along dorso-anterior

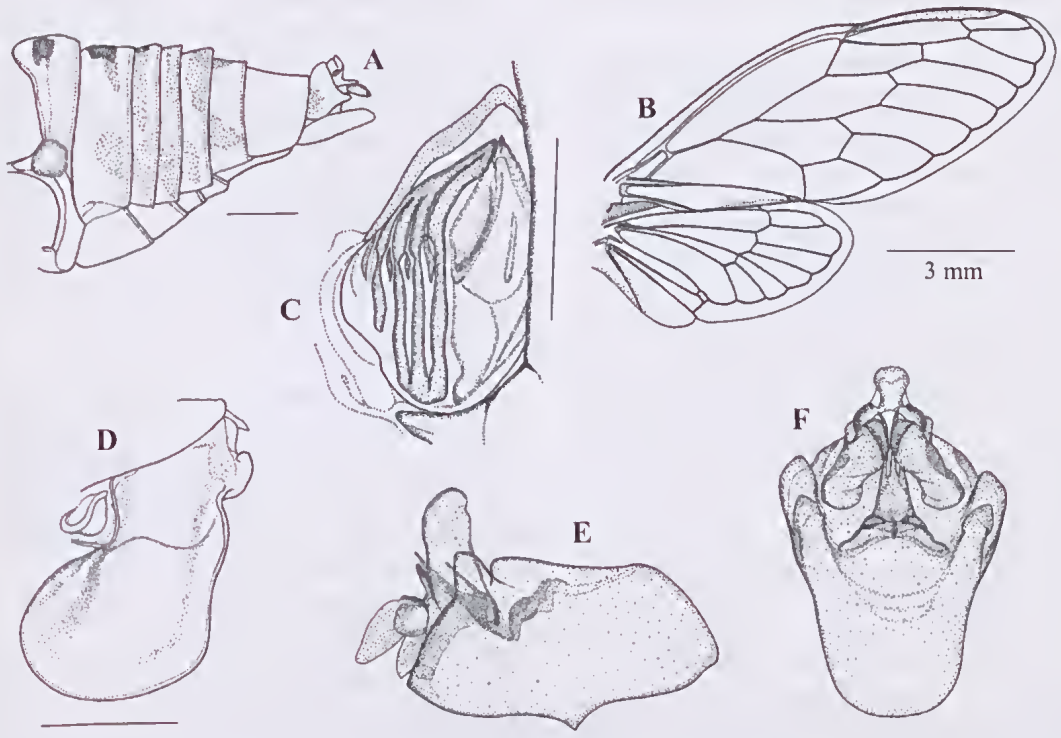


FIG. 6. *Crotopsalta poaecetes*. A, Lateral abdomen view; B, fore and hind wings; C, timbal; the right-hand edge as shown represents the posterior margin, the top the dorsal edge; D, opereula; E, and F, lateral and ventral views of pygofer. Pygofer length 1.4mm. Scale bars represent 1mm exeept wings (3mm). Drawings from speeimens from Cloncurry, northwestern Queensland.

margin of plate, extending around bases of antennae. Oeelli red. Compound eyes dark brown. Gena and mandibular plate pale sandy brown, with narrow black margin adjaeent to anteelypeus; silver pubeseenee conspicuous. Postelypeus with anterior eentral area entirely pale yellow-brown, enclosed by a narrow and diseontinuous dark brown to black marginal zone; black to dark brown transverse ridges; remaining area pale sandy brown. Anteelypeus pale sandy brown with small eentral brown area. Rostrum sandy brown grading to darker brown apieally and along eentral suture. Antennae dark brown, paler apieally.

*Thorax*. Pale sandy brown and dark brown. Pronotum and pronotal eollar entirely pale sandy brown; pronotal eollar along lateral margin weakly ampliate. Mesonotum with a pair of anterior obeonieal, short, brown and broad paramedial faseiae, fused medially, with diffuse distal terminations whieh extend distally approximately one-third of the length of the mesonotum; a pair of broad, oblique lateral brown faseiae, diffusively terminated anteriorly, inward pointing distally; a pair of thin brown oblique faseiae between the two sets of broad faseiae (i.e. lateral and paramedial); a black, irregular eentral spot anterior to the erueiform elevation; remaining areas pale sandy brown, ineluding the erueiform elevation and the wing grooves, the latter with marginal silver pubeseenee.

*Wings*. Fore wing venation very pale yellow-brown to translueent; elearly developed node on eostal vein; eostal vein exhibits gentle but quite distinet anterior eurvature; pterostigma pale yellow brown, translueent; basal membrane pale sandy brown. Hind wing colouration as in fore wing; plaga opaque white, extending adjaeent to 3A vein.

*Legs*. Dominantly pale sandy brown. Foreleg tarsi tending darker brown. Thin pale to medium brown longitudinal faseiae are present along the anterio-dorsal margins of the fore and mid

femora; three dark brown spines on fore femora. Claws dark brown apically.

*Operculae*. Elongated but slightly expanded and rounded at distal-medial margins; entirely pale sandy brown except for a small pale brown area adjacent to crest around distolateral margins; meracantha rounded and poorly developed.

*Timbals*. Ribs 1-3 extend across timbal; anterior rib 5 very short; rib 4 intermediate in length, not fused to ribs 1-3 ventrally; four short ridges.

*Abdomen*. Tergites dominantly sandy brown, grading to pale brown distally; diffuse black to brown medio-dorsal areas, which are most extensive on tergite 2, becoming progressively smaller and paler towards tergite 7; these darker areas do not extend to distal tergite margins; auditory capsules pale sandy brown, rarely with small brown marking adjacent to central areas; brown diffuse lateral patches on tergites 3 to 4, becoming more weakly developed distally. Sternites II and III pale sandy brown, grading to pale brown towards sternites VII and VIII.

*Genitalia*. Pygofer variable pale to medium brown. Otherwise as in generic description.

FEMALE. Fig. 39B. Similar to male but with reduced areas of darker colouration. Supra-antennal plate as in male, with decreased black colouration along distal and lateral margins. Postclypeus as in male but with the areas of brown colouration paler and reduced in extent. Pronotum as in male. Mesonotum similar to male with reduction in size of anterior obconical fasciae which are not fused medially, and are paler brown; the lateral oblique fasciae are paler brown and fragmented in extent; two small brown spots adjacent to anterior arms of cruciform elevation. Legs pale sandy brown with apices of claws brown. Tergites pale sandy brown, with paramedial darker brown areas on tergites 2-4, which are paler and greatly reduced on tergite 4, and absent on tergites 5-9; dorsal surface of tergites with well defined pale sandy brown, with fine silver pubescence, giving overall appearance of weak dorsal fasciae; diffuse pale brownish ventrolateral patches on tergites 3-7. Sternites pale sandy brown. Ovipositor sheath extends ~0.5 mm beyond tergite 9.

MEASUREMENTS. N = 10♂, 9♀. *BL*: ♂ 8.7-10.8 (10.0); ♀ 10.4-10.9 (10.7). *FWL*: ♂ 9.9-11.4 (10.7); ♀ 11.4-12.2 (11.8). *HW*: ♂ 2.5-3.0 (2.8); ♀ 2.7-3.0 (2.9). *PW*: ♂ 2.4-2.8 (2.7); ♀ 2.8-3.1 (2.9). *AW*: ♂ 2.8-3.3 (3.1); ♀ 2.9-3.3 (3.1). *FWL/BR*: ♂ 2.33-2.87 (2.57); ♀ 2.42-2.83 (2.63).

DISTRIBUTION, HABITAT & BEHAVIOUR (Fig. 2). A species restricted to open grassland and grassland in open forest, occurring in northwest Queensland. It occurs in a variety of grass species including buffel grass (*Cenchrus ciliaris*), Queensland bluegrass (*Dichanthium sericeum* ), and silky browntop (*Eulalia aurea*). This cicada is wary, highly cryptic and readily flies, singing whilst sitting on grass stems and in associated forbs. The species is most widespread in the Cloncurry region, extending to Dajarra and Quamby, but is not recorded from Mt. Isa.

ETYMOLOGY. Greek *poa* and *ecetes*, grass dweller.

SONG (Figs 7-11; Table 2). A relatively slow ticking song, generally intermediate between the *C. plexis* and *C. fronsecetes* tick rates, ranging between 3.5-6.9 per second($s^{-1}$). The ticks aurally sound to be single ticks, but when examined at higher resolution, comprise distinct double pulses of nearly equal amplitude.

## ANALYSIS OF THE TICKING SONGS OF *CROTOPSALTA* CICADAS

The genus is characterised by relatively simple ticking songs. Although a number of other Queensland species have tick-like songs (e.g. *Pauropsalta dubia* Goding & Froggatt; *P. emma* Goding & Froggatt; *Urabunana marshalli* Distant; *U. segmentaria* Distant; and others decribed below), detailed analyses of most of these songs reveals their tick-like structure to be more complex than those described in *Crotopsalta*, and are more appropriately termed chirps (Ewart, 1998). The four *Crotopsalta* species described occur within relatively diverse habitats and regions, and their ticking songs cannot be correlated with specific habitat types. The cicadas are, however, all very small and highly mobile in their behaviour patterns, but these attributes are common in other small Australian cicadas, some of which have significantly more complex songs (e.g. *U. verna* Distant; *Cicadetta murrayensis* Distant; Ewart & Popple, 2001). Such ticking songs are significant in the context of their apparent simplicity and therefore apparently limited potential for evolution of inter-specific song variations. Two variables that seem to have been exploited, however, are the pulse repetition rates and the detailed pulse structures.

Waveform and envelope plots of the songs are shown in Figs 7-9, and amplitude spectra of the songs in Fig. 10. Comparative details of the ticking songs (Table 2), indicate the following:

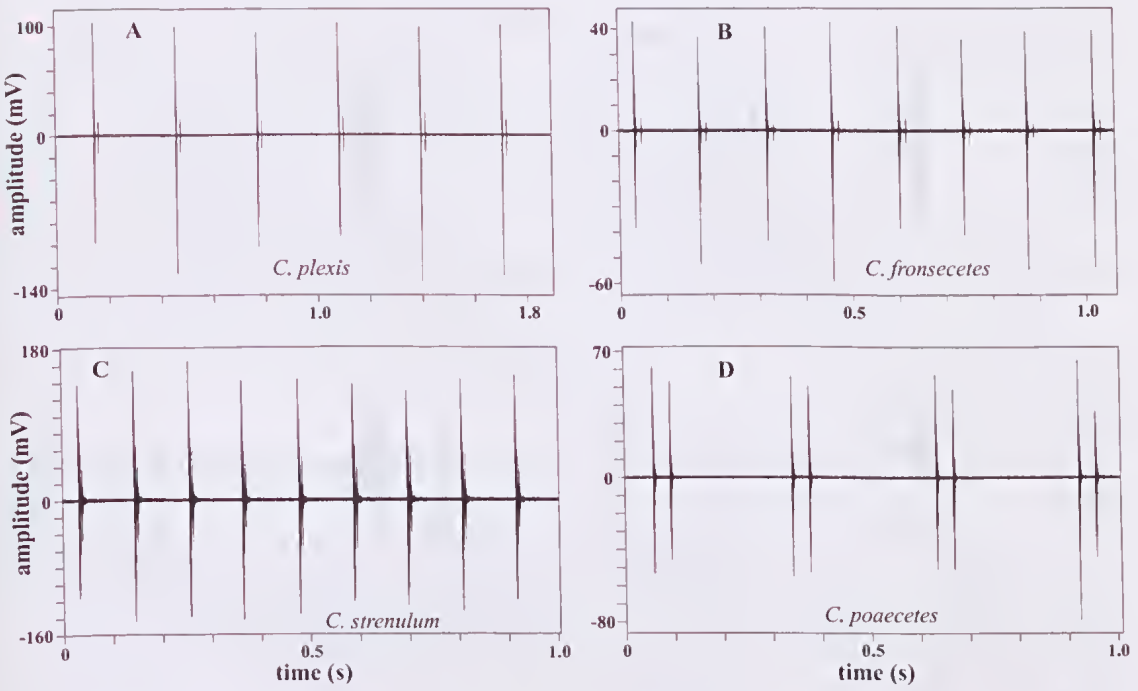


FIG. 7. Waveform plots, comparing the broader pulse structures of the four *Crotopsalta* ticking cicadas: (a) *C. plexis*, from 31km W. of Mitchell. (b) *C. fronsecetes*, 41km southeast of Childers. (c) *C. strenulum*, 5.7km east of summit of Expedition Range, west of Bauhinia, central Queensland. (d) *C. poaecetes*. Dajarra, northwestern Queensland. Each figure represents a recording made of insects within a container. The data have each been filtered (FIR) to 1kHz.

(a) In all species, each tick structure comprises two (or sometimes three in *C. poaecetes*) distinct pulses which in Fig. 9 are numbered 1 and 2 (and 3 in the *C. poaecetes* plot). With the exception of some of *C. poaecetes* songs, the second pulse has a reduced amplitude (weakest in *C. fronsecetes*), resembling the simple 'hand operated' timbal 'in-out' movements illustrated by Josephson & Young (1985). In *C. strenulum*, the two pulses may partially coalesce or be separated (less common). In *C. poaecetes*, the amplitudes of pulses 1, 2 and 3 are variable. If pulses 2 and 3 have coalesced, their combined amplitude is similar to pulse 1. If pulses 2 and 3 are separated, their amplitudes are reduced relative to pulse 1 (Fig. 9E). Attention is drawn to the differences in detailed timbal structures of *C. poaecetes* compared to the other three species, notably the rib 4 that is clearly separate from ribs 1-3. This suggests that the independent role of rib 4 could be significant in the generation of pulses 2 or 3. In contrast, the ventral fusion (or near fusion) of ribs 1-4 in the other three species (see above) suggests that these act in unison during the initial 'in' movement of the timbal in producing pulse 1, and similarly for the fused ribs 1-3 in *C. poaecetes*.

(b) Pulse repetition rates vary between all four species, with some overlap occurring between *C. fronsecetes* and *C. strenulum* songs. It is clear, however, that temperature does affect the pulse rates. Temperatures within the recording boxes fall into a relatively narrow range (30-35°C) as previously noted. Field recordings cannot be constrained in terms of the insect temperatures as these were made of insects singing in open sunlight and in partial and constantly varying shade conditions (e.g. in moving tree foliage), typically at shade temperatures in excess of 30°C. Comparison of container and field recordings (Table 2; Fig. 11) indicate that the pulse rates are higher in field recordings, although they do not greatly differ for *C. plexis* and *C. fronsecetes*, but are more significant for *C. strenulum*. Reasons for these differences are attributed to the microhabitats of the respective species, with *C.*

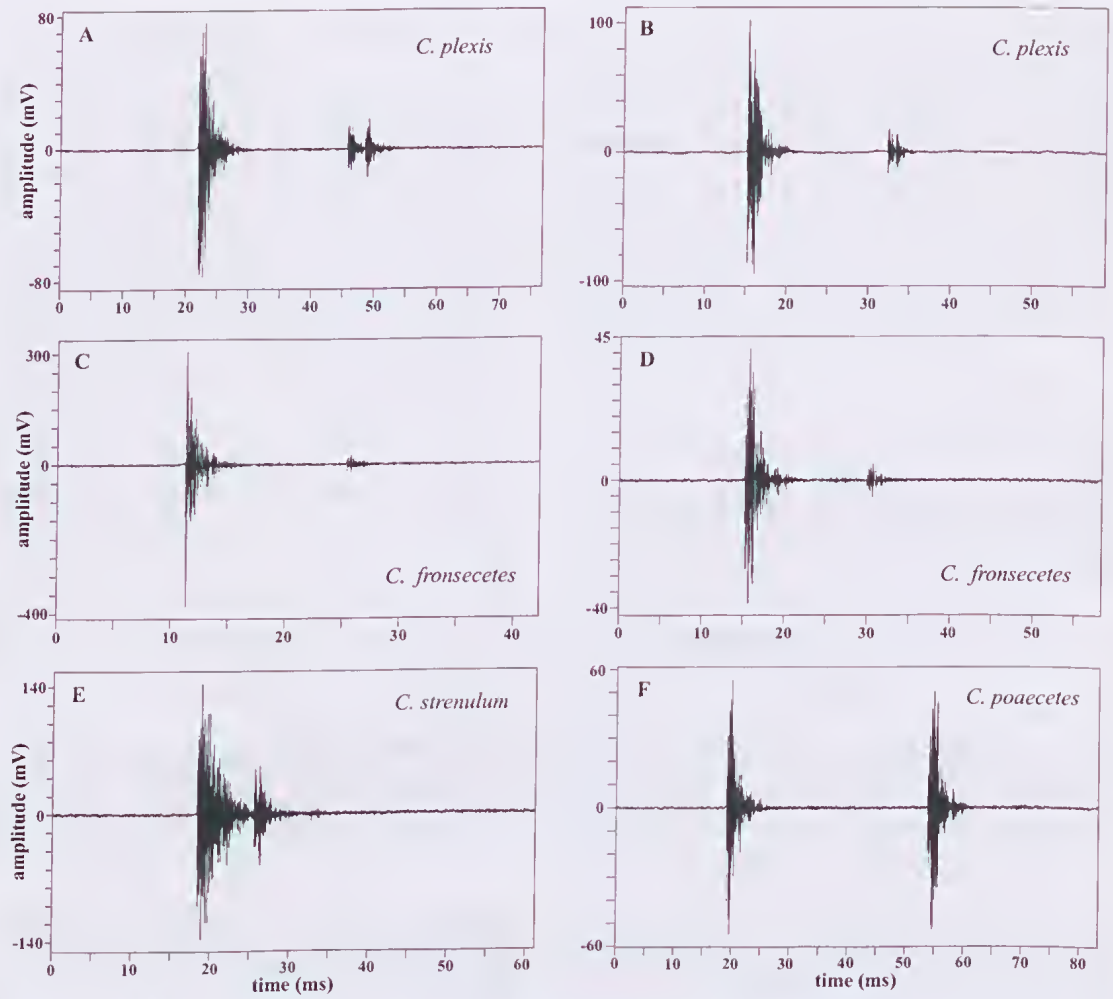


FIG. 8. Expanded waveform plots comparing further detail of individual pulse structures of the four *Crotopsalta* ticking cicadas. (a) and (b), *C. plexis*, from Kaimkillenbun, near Dalby, and 31km west of Mitchell, respectively. (c) and (d), *C. fronsecetes* from Gurulmundi, near Miles, and 41km southeast of Childers, respectively. (d) *C. strenulum*, location as in Fig. 7C. (d) *C. poaecetes*, location as in Fig. 7D. Each based on container recordings, each filtered (FIR) to 1kHz.

strenulum, a grassland species, frequently singing in open sunlight. In contrast, *C. plexis* and *C. fronsecetes* sing within foliage under variable shaded conditions. The tick rates provide important field criteria for species identification.

(c) Length of pulses 1 and 2 are very similar (Table 2) in each species, consistent with a similar mechanism of generation. Pulse 3 in *C. poaecetes* is slightly longer than the pulse 2 length. The inter-pulse intervals (time duration between start of pulses 1 and 2; Fig. 11; Table 2) exhibit differences between species, noting the overlap between *C. plexis* and *C. fronsecetes*. The partial differences in pulse repetition rates and inter-pulse intervals suggests that the combination of these two variables can be used to separate the four species. In Fig. 11 the data are subdivided according to container versus field recordings, and the data fields indicate systematic differences, and variability, between and within species, especially when considering the field and container data separately. Importantly, differences between tick rates and pulse structures are discernible and are therefore presumably utilised in species recognition.

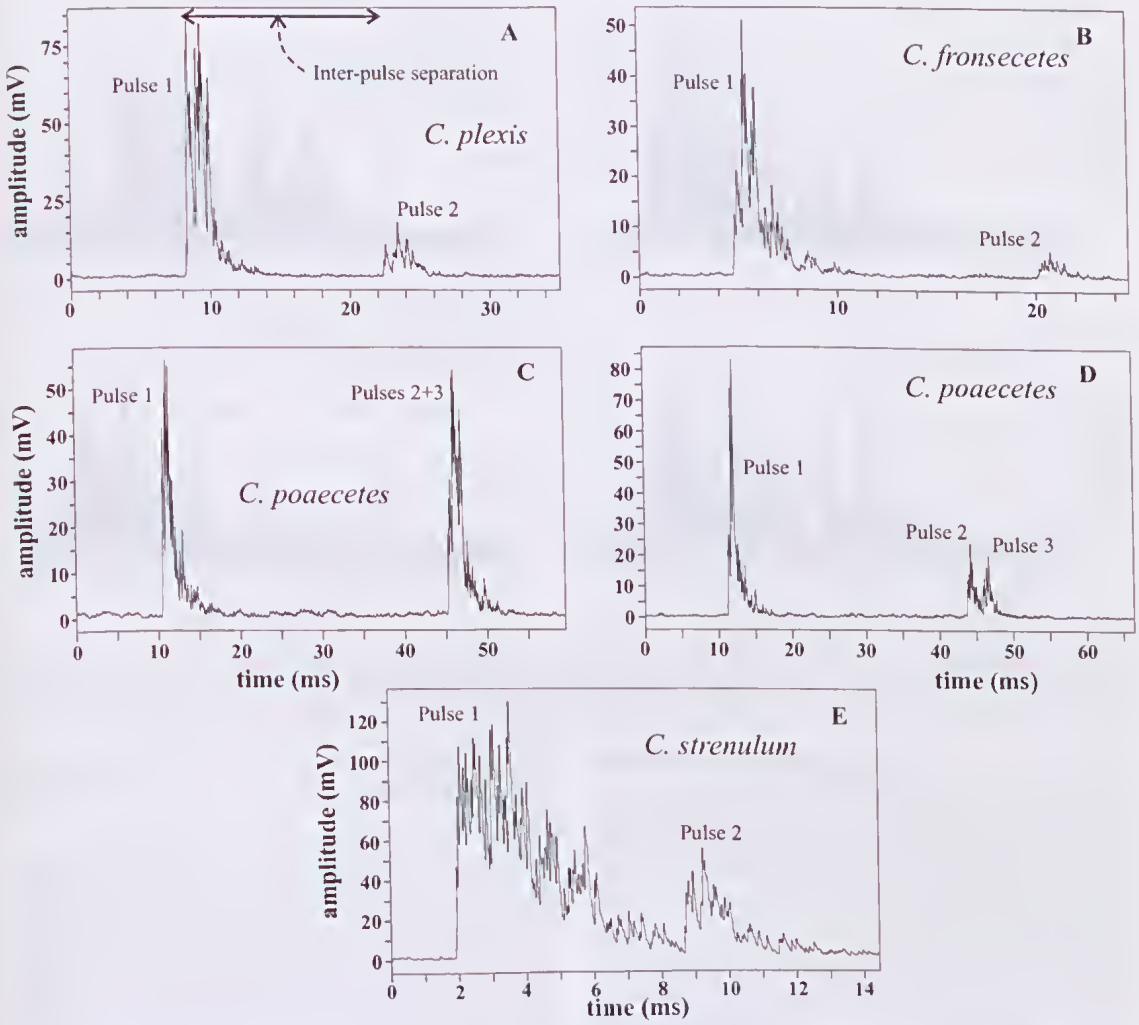


FIG. 9. Expanded envelope curves showing higher resolution structures of the ticking pulses, and the definitions used in the text for the inter-pulse separation intervals, and pulse numbering. (a) *C. plexis*, location as in Fig. 7A. (b) *C. fronsecetes*, location as in Fig. 7B. (c) and (d) *C. poaecetes*, from Dajarra and 34km east of Cloncurry, respectively. In (c), the coalescence of pulses 2 and 3 produce a higher amplitude second pulse, compared to (d), in which pulses 2 and 3 are separated, each with lower amplitudes. (e) *C. strenulum*, location as in Fig. 7C. Each plot based on container recordings, each filtered (FIR) to 1kHz.

These differences are emphasised by other variations in pulse structures in their respective envelope curves (Fig. 9A-E), especially notable in *C. strenulum* and *C. poaecetes*.

(d) Time expanded envelope curves (Fig. 9) indicate very abrupt initiation to the first pulses of the ticks, with the possible exception of *C. fronsecetes*, with the second pulse generally also exhibiting relatively sharp initiations. The structures of individual pulses illustrate further complexities. Pulse 1 of *C. plexis*, for example, exhibits at least four distinct 'carrier pulse' phases. The damping of the individual pulses seems to approximate logarithmic decay curves, with the exception of *C. strenulum* in which pulse 1 follows a more linear damping.

(e) Amplitude spectra (Fig. 10) are complex, showing a series of broad frequency peaks occurring between approximately 4 to near 18kHz (the latter the limit of recording

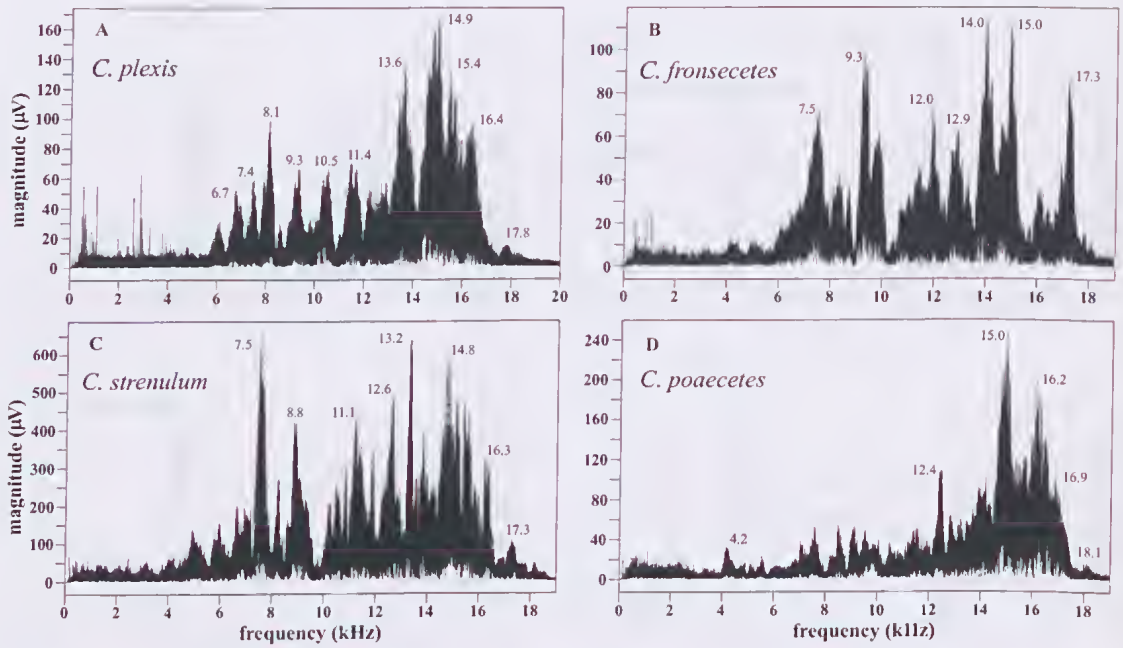


FIG. 10. Amplitude spectra of the songs of the four *Crotopsalta* ticking cicadas. (a) *C. plexis*; (b) *C. fronsecetes*; (c) *C. strenulum*; (d) *C. poaecetes*. Locations and other details as in Fig. 7A-D, respectively. Frequencies of the main peaks are labelled (kHz). Recordings filtered (FIR) to 0.5kHz.

capability). Carrier frequencies of ≥ 14kHz are verified by counts of resolvable carrier pulses in the amplitude envelope curves. The width of the spectral peaks is attributable to the short duration of the constituent sinusoidal pulses. The spectra indicate no regular sequence of harmonic or side band peak sets, but there is nevertheless a crude periodicity in the modulation and grouping of the peaks in each species, averaging approximately 1kHz. Specifically for *C. plexis*, *C. fronsecetes*, *C., strenulum* and *C. poaecetes*, the means and ranges of the observed periodicities are, respectively (kHz): 1.066 (0.74-1.34); 1.09 (0.84-1.29); 1.07 (0.78-1.24); and 1.10 (0.58-1.47). The detailed irregularities suggest frequency overtones. It is important to note that the various frequency peaks are not present in the background spectra, and are characteristics only of the ticking songs, which clearly represent complex periodic waves.

(f) The modulation frequencies defined by the pulse repetition rates, the inter-pulse intervals and the pulse lengths lie in the range of approximately 2-300Hz. These are very low frequencies compared to the carrier frequencies and are strongly developed in the amplitude spectra as line spectra that decrease irregularly in amplitude with increasing frequency. They are generally weakly developed above 1kHz and for clarity are filtered out in the spectra shown (Fig. 10).

(g) The amplitude differences between pulses 1 and 2 have been noted above. These differences extend to the separate amplitude spectra prepared separately for each of the pulses. Comparison between pulse 1 and the composite amplitude spectra made of multiple pulses (Fig. 10) reveals good correspondence between the main peaks, as expected by the higher amplitude of pulse 1. Comparison of the spectra between pulses 1 and 2, however, reveals many detailed discrepancies in the frequencies of the main peaks. For example, in *C. plexis*, *C. fronsecetes*, *C. strenulum* and *C. poaecetes*, respectively, only 9 close coincidences are observed out of the total of 22 combined peaks; 9 out of 17 peaks; 6 out of 22 peaks; and 9 out of 17 peaks. These point to a variation in their mechanisms of generation and/or radiation. One plausible explanation for pulse 2 is by the 'clicking back' of the timbal, representing changed stress conditions (Bennet-Clark, 1997; Fonseca & Popov, 1994). In this scenario, the maximum amplitude of vibration of the timbals during their outward buckle is not as close, relative to pulse 1, to the natural resonance frequency of the relevant parts

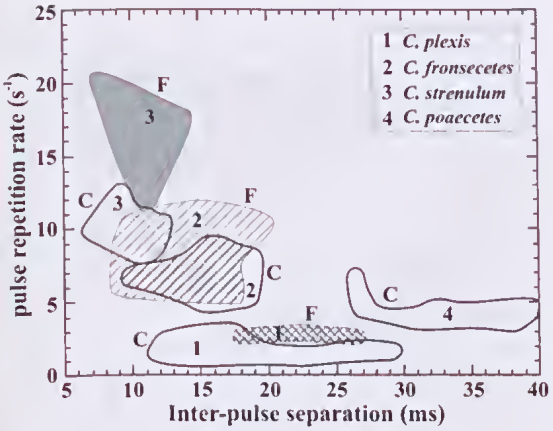


FIG. 11. Plots of pulse repetition rate versus inter-pulse separation of the songs of the four *Crotopsalta* ticking cicadas. Data subdivided into field recordings (F; enclosed fields with fill) and container recordings (C; enclosed fields without fill).

of the body (e.g. timbals, abdominal cavity, and tympana) responsible for radiating the sounds (Bennet-Clark, 1997; Fonseca & Popov, 1994), i.e. the impedance of the sound radiating structures is higher and the forced amplitude of the body systems correspondingly reduced.

(h)The mean maximum and mean frequencies measured are >13kHz for each species (Table 1), but as shown above, the ticking songs are very broadband, with distinct lower frequency peaks. It needs to be noted that the frequency ranges (Fig. 10) underestimate the higher frequency range of the emitted ticks, as bat detector field observations indicate that at close range, frequencies extend (albeit weakly) to 45-60kHz. The lower frequency peaks in the spectra of such small cicadas are significant in view of the correlation between decreasing body size and increasing song frequencies (e.g. Bennet-Clark & Young, 1994; Bradbury & Vehrencamp, 1998). Broadening of frequencies are, however, characteristic of short and very sharp signals (e.g. Bradbury & Vehrencamp, 1998). Fonseca & Popov (1994), in their detailed study of the similarly small Portugese cicada, *Tympanistalna gastrica* Stål, showed that several separate structures contribute differently to the radiation of clicks and soft pulses. The timbals are the main radiators of the dominant spectral peaks at 10-11kHz (clicks) and 12-13kHz (soft pulses), the tympana are important in radiation of frequencies both below and above the timbal peaks, while the abdomen is more important in click generation at lower frequencies of approximately 5kHz. The overall song of *T. gastrica* is more complex than the ticking cicadas described here, but the occurrence of the wide range of frequency peaks of the clicking pulses has close similarities.

## POSSIBLE SIGNIFICANCE OF TICKING SONGS

Ticking songs represent the most cryptic and simplest of periodic patterns, characterised by low amplitudes (at least below 18kHz), a very high degree of redundancy and broad frequency spectra, the latter producing marked ventriloquial effects in the field. These attributes, when coupled to the highly mobile behaviour of the cicadas, negates the need for long distance sound transmission (e.g. Römer & Lewald, 1992). The simple patterns are thought relatively robust to temporal degradation during sound transmission (based on bat detector field recordings), and may also minimise predation, the latter further aided by the small size, soft calls, cryptic nature and mobility of the *Crotopsalta* cicadas. As noted above, field observations with a bat detector indicate that at close range, frequencies extend (albeit weakly) to 45-60 kHz. The wide frequency range of the songs should, however, facilitate more efficient survival of the essential form of the signal due to loss and degradation by absorption, scattering, boundary reflections and refraction during propagation, all of which are frequency dependant. Bat detector observations confirm their strongly reflective properties from the ground and surrounding vegetation without obvious distortion. The wide frequency range also provides an effective way to minimise induced amplitude modulations due to wind movement and turbulence within tree foliage, together with frequency filtering of sound propagating through foliage (e.g. Michelsen, 1992, Römer, 1992, 1993; Stephen & Hartley, 1991; Richards & Wiley, 1980; Michelsen & Larsen, 1983; Römer & Lewald, 1992). In their study of the propagation of pure tone bursts of 15 kHz frequency with variable duration (0.5-2 ms, at 100 ms inter-burst intervals), comparable to the ticking songs considered here, Stephen & Hartley (1991) showed that pulses of increased duration propagated better, i.e. the relative amplitudes of the lower frequency segment of the envelope spectrum were increased. At constant duration (1ms), increasing distance results in shrinking of the signal coherence until at ≥4 m, only the

15kHz carrier frequency remained coherent. In the case of the *Crotopsalta* ticking songs, the broadband frequencies will presumably offset the predicted degradation effects. A further potential value of the highest frequency components of the ticking pulses is in sound localisation (Gerhardt & Huber, 2002).

The inferred properties of the ticking songs are therefore suggested to represent very flexible recognition signals. Combined with the mobility and small size of the cicadas, these attributes should minimise predation. In fact, field observations suggest that capture in spider webs is perhaps the major predation threat. The pulse repetition rates and pulse structures appear to provide the differential characteristics that are utilised for inter-specific song recognition.

**Gagatopsalta** gen. nov.

TYPE SPECIES. *Gagatopsalta auranti* sp. nov.

INCLUDED SPECIES. *G. auranti* sp. nov.; *G. obscurus* sp. nov.

ETYMOLOGY. Greek *gagat,* referring to the prominent shiny/jet black appearance of extensive areas of the bodies of the two described species.

DIAGNOSIS. Small cicadas, 10-13.5 mm total body length. Head and thorax broadly 'cylindrical' in form; distance between lateral ocelli similar to distance between lateral ocellus and eye; head width (across eyes) slightly greater than width of pronotum across lateral margins; abdomen cylindrical, gently curving into pygofer in dorsal view; pronotal collar markedly ampliate along lateral margins and outwardly curved; width of pronotum measured from lateral margins similar to width of mesonotum measured between fore wings. Head, thorax and tergites predominantly a distinctive shiny (jet) black, with subordinate orange-brown and/or yellow-orange markings. Rostrum extends to between mid and hind coxae. Wings hyaline, without infuscation; fore wing costal vein even in width to node, with gentle anterior curvature proximal to node; sclerotised anterior area of costal vein narrow, less than costa thickness; intersection of CuA with M veins occurs approximately one third to midway along length of the first vein section (proximal to basal cell) of the M vein (that lies along inner margin of radial cell); the three distal vein sections that make up the inner margins of the radial cell are all of unequal length; 8 apical cells, which are, overall, similar in length to the ulnar cells (some shorter, some longer). Hind wing with 6 apical cells. Operculae weakly elongated with a marked ridge extending longitudinally along anterio-lateral half of each opercula to, and terminating in distal area; rounded along distal to medial margins; meracantha prominent, relatively acutely terminated, extending over distal area of opercula, and located asymmetrically towards midline, near or at the inner margins of operculae; inner margins of opposite opercula widely separated. Abdomen with sternites rounded and mostly projecting below the level of tergites in lateral view. Timbals with five long ribs, ribs 1 to 2 fused ventrally; four short ribs; dome on timbal plate lozenge-shaped, somewhat elongated; distinct basal spur into which ribs 1 to 3 are fused dorsally. Pygofer broadly ovoid when viewed dorsally; upper lobe prominent, extended distally, with rounded termination; lower lobe partially hidden behind upper lobe in lateral view; inner lobe prominent, somewhat rounded and extended ventrally; uncal lobes sharply terminated and extended anteriorly; prominent and rounded median process; beak relatively short and obtusely terminated. Aedeagus trifid with prominent sclerotised pseudoparameres, sharply terminated apically; sclerotised shorter ventral support and poorly sclerotised endotheca.

**Gagatopsalta auranti** sp. nov.
(Figs 12, 13, 15, 17, 19, 20, 40, Table 3)

*Notopsalta* sp. H: Ewart, 1998: 64, 65, figs.9A, 14C.

MATERIAL. HOLOTYPE; ♂, QMT99213, Barakula S.F., nr. Chinchilla, S.Q., Virgin brigalow, 15 Dec 1997, 26°14.42'S 150°48.86'E, Ewart, Recorded.

PARATYPES: SOUTHEAST QUEENSLAND: 31♂, 30♀, Brigalow, 1km E Brigalow Township, AE, 22.xii.2001, 26°50.94'S 150°47.83'E; 2♂, 14♀, Brigalow-belah, 'Lakeview', nr. L Broadwater, via Dalby, AE, 20.xii.2001, 27°81'S 151°04.98'E; 27♂, 51♀, Brigalow, L Broadwater, via Dalby, AE, 19.xii.2001, 27°20.42'S 151°05.65'E; 1♂, As previously, Rec spec 1; 1♂, As previously, Rec spec 2; 1♀, 'Allinga' pty, N. Chinchilla, brigalow, AE, 9.i.2002, 26°39.79'S 150°38.06'E; 29♂, 24♀, 'Allinga', Lithgow Rd., Chinchilla, 8.i.1994; 1?, Brigalow Res. Stn., nr. Theodore, NW Brigalow section, 18.xii.2000, AE, 24°47.93'S 149°45.45'E, Rec; 1♂, 5♀, Barakula SF, nr. Chinchilla, virgin brigalow, 15.xii.1997, 26°14.42'S 150°48.86'E, AE; 1♂, As previously, Rec spec 1; 1♂, As previously, Rec spec 2; 3♀, Brigalow Res. Stn., nr. Theodore, E brigalow section, 19.xii.2000, AE, 24°48.85'S 149°47.48'E; 1♂, As previously, Rec **(AE)**. 1♀, Kalbar, 17.xii.1998, JM, LWP, MV lamp. 367-0001 **(LWP)**. 1♀, 26°13'S, 150°35'E, Barakula, 23 km NNE, 18.xii.2001, GBM, DC, SW, brigalow, 400m, 10313; 1♂, 25°10'S, 150°01'E, Isla Gorge

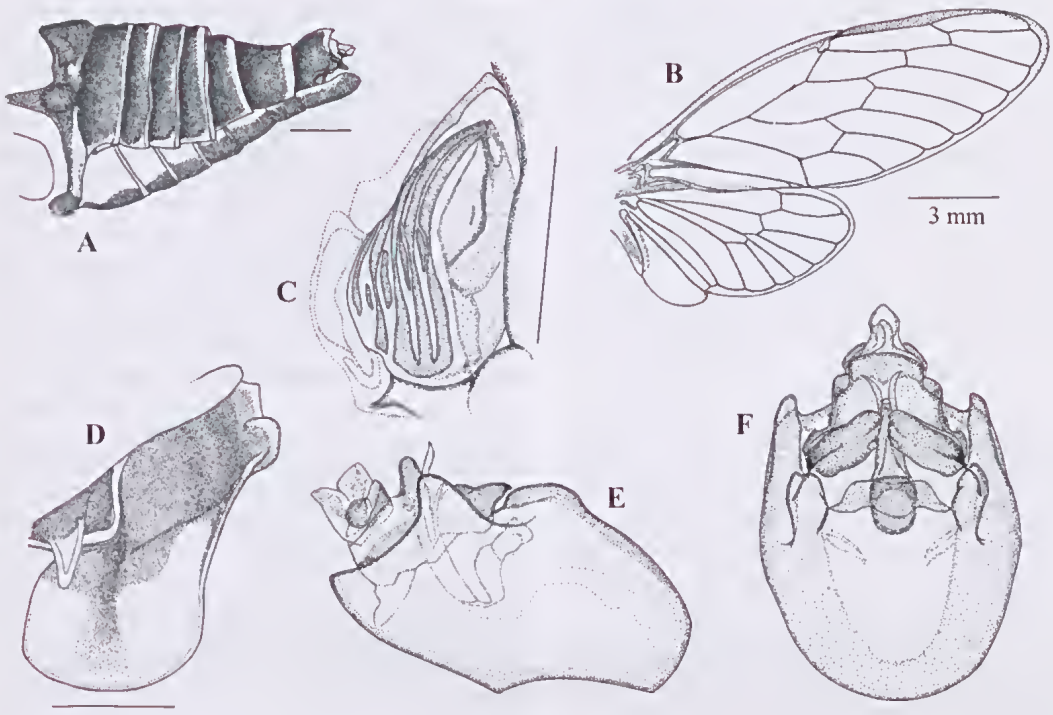


FIG. 12. *G. auranti*. A, Lateral abdomen view; B, fore and hind wings; C, timbal; the right-hand edge as shown represents the posterior margin, the top the dorsal edge; D, opereula; E, and F, lateral and ventral views of pygofer. Pygofer length 2.1mm. Scale bars = 1mm exeept wings (3mm). Drawings based on specimens from the northern Barakula State Forest, north of Chinchilla, and near Chinchilla (genitalia only).

NP, NE corner, 240m., 3.iii.1998, Mv lamp, CB, SE **(QM)**. 1♂, 1♀, brigalow, L Broadwater, via Dalby, AE 19.xii.2001, 27°20.42'S 151°05.65'E **(BMNH)**. 1♂, 1♀, brigalow, L Broadwater, via Dalby, AE, 19.xii.2001, 27°20.42'S 151°05.65'E **(ANIC)**. 1♂, 1♀, brigalow-belah, 'Lakeview', nr. L Broadwater, via Dalby, AE, 20.xii.2001, 27°81'S 151°04.98'E **(MSM)**.

DIAGNOSIS. Given under *G. obscurus* sp. nov.

DESCRIPTION (Male). Figs 12, 40A. *Head.* Supra-antennal plate shiny black with small lanceolate medial, sandy brown fascia, anteriorly pointing, extending from distal margin of plate (between the lateral ocelli), terminating proximally to the anterior ocellus; small discontinuous sandy brown spots extend along the anterior dorsal margin of the plate, adjacent to the postclypeus, but not reaching to the bases of the antennae. Ocelli pink to pale red. Gena and mandibular plate shiny black with conspicuous silver pubescence. Postclypeus dominantly shiny black including transverse ridges, with a very small and short pale sandy brown fascia in medial anterior area, extending in some specimens to the dorsal postclypeal surface as a triangular pale brown area, a narrow but well defined pale sandy brown margin encloses the frons. Anteclypeus shiny black with small dark brown dorso-medial area. Compound eyes dark brown, their outer distal margins clearly separated from pronotum. Rostrum medium brown grading to black apically. Antennae dark brown to black.

*Thorax.* Pronotum shiny black with small orange-brown central fascia which extends from anterior to approximately one half (or less) the distance to the posterior margin; pronotal collar entirely shiny black. Mesonotum with a pair of anterior short, broad obconical, shiny black paramedial fasciae, completely fused medially, extending from the pronotal collar distally for approximately one quarter of the length towards

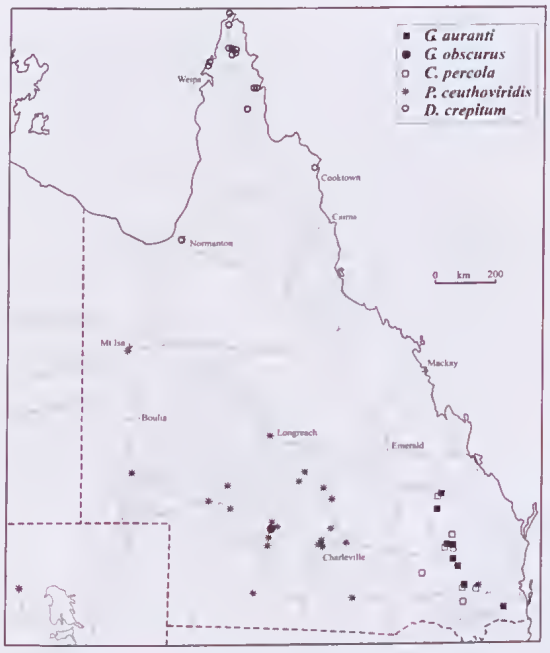


FIG. 13. Distribution records of the five new species of 'chirping' cicadas belonging to the genera *Gagatopsalta, Pipilopsalta, Caliginopsalta,* and *Drymopsalt*a, through Queensland and northeastern South Australia.

the distal margin; extending distally from these fused fasciae is a broad medial black fascia which extends to, and abruptly expands into, the anterior margin of the cruciform elevation; this fascia continues as a dark brown triangular marking across the cruciform elevation, narrowing and terminating at the distal mesonotum margin; a pair of black spots occur between the anterior arms of the cruciform elevation; a pair of broad shiny black lateral fasciae extend distally from the pronotal collar, tapering and subacutely terminated distally, to near but not reaching the anterior cruciform elevation arms; the margins of these fasciae are sharp but crenulated, especially along medial margins; remainder of mesonotum and wing grooves bright orange.

*Wings.* Fore wings with costa and R+Sc veins bright orange grading to pale brown distally along the R+Sc vein; remaining venation orange-brown proximal to wing bases grading to dark brown apically; basal membrane bright orange; costal vein gently curved; pterostigma with dark reddish-brown infuscation, extending weakly along anterior wing margin towards apex. Hind wing with veins pale orange-brown proximally, grading to medium brown distally; plaga orange which extends along 3A vein; central area of plaga with brown infuscation.

*Legs.* Coxae shiny black along anterior and lateral edges, changing to orange on and proximal to the trochanters, with additional orange along corners of fore coxae. Fore femora orange with three black spines, and black around and joining the bases of the spines; mid femora orange with broad diffuse brown longitudinal fasciae along lateral margin; hind femora orange. Tibiae and tarsi of fore legs dominantly orange to orange-brown. Pretarsal claws orange to orange-brown with dark brown to black tips.

*Operculae.* Distal areas orange-brown becoming shiny black proximal to and along medial sutures, and extending across most of the basal part except for the small pale brown crest at the dorsolateral corners; shapes broadly rounded along distal margins, becoming initially relatively linear and then relatively sharply rounded towards and around the medial margins; operculae do not extend to paramedial anterior margin of sternite II, when viewed laterally.

*Timbals.* Ribs 4 and 5 not fused ventrally to ribs 1-3; rib 4 extends across timbal, while rib 5 extends only partially across timbal.

*Pygofer.* Refer to generic characters.

*Abdomen.* Sternites visible in lateral view. Tergites dominantly shiny black with short sparse silver pubescence; tergite 2 with slightly diffuse narrow orange-brown distal margin extending completely across tergite; tergites 3-7 with sharply defined, relatively narrow orange-brown to pale brown distal margins extending completely across each tergite; tergite 8 black, grading to pale brown along paramedial and lateral margins; auditory capsules mainly black with small pale brown ventro-medial areas. Sternite II orange-brown along lateral and paramedial margins, shiny black along anterior margin and medially; sternites III-VII orange-brown laterally, with broad black medial area, each brown along distal edge; the general appearance is of a broad, clearly defined black longitudinal median fascia along abdominal ventral surface; sternite VIII black, grading to pale brown along lateral edges.

FEMALE. Fig. 40B. Colour shiny black and orange, similar to male. Pronotum, mesonotum, wings and leg markings very similar to male. Tergites 3-7 similar to male; tergite 2 shiny black with narrow diffuse orange-brown distal margin,

becoming broader laterally; tergite 8 shiny black with orange-brown distal margin, narrow medially but broadening irregularly laterally; tergite 9 orange-with shiny black medial and anterio-lateral area, narrow black ventral edges, and a prominent black spot disto-laterally; junctions between the black and orange colourations very irregular. Sternites II-VII orange-brown laterally, each with a well defined black medial area which rapidly narrows, and becomes paler proximal to the distal margins; these give the general appearance of a broad black longitudinal fascia extending along the sternites. Ovipositor sheath extends approximately 0.5 mm beyond the distal edge of tergite 9.

MEASUREMENTS. N = 10♂, 10♀. *BL*: ♂ 9.8-12.3 (10.8); ♀ 10.7-12.8 (11.6). *FWL*: ♂ 13.2-15.2 (14.1); ♀ 14.2-16.4 (15.6). *HW*: ♂ 3.6-4.3 (3.9); ♀ 3.9-4.4 (4.2). *PW*: ♂ 3.0-3.7 (3.3); ♀ 3.4-4.0 (3.6). *AW*: ♂ 3.3-4.0 (3.6); ♀ 3.2-4.2 (3.7). *FWL/BR*: ♂ 2.62-2.80 (2.71); ♀ 2.64-2.88 (2.75).

DISTRIBUTION & HABITAT (Fig. 13). Restricted to brigalow (*Acacia harpophylla*) in southeast Queensland. Known locations extend southwards from Isla Gorge National Park to Theodore (Brigalow Research Station) to the Chinchilla-Dalby region, including the Barakula State Forest, and to Kalbar. It is anticipated that its occurrence will extend more widely through the brigalow regions. Emergences most commonly coincide with summer rains during mid December to mid January, with one specimen taken in early March (Isla Gorge). It is an inconspicuous species inhabiting brigalow foliage, normally caught only at light.

ETYMOLOGY. Latin *auranti*, referring to the bright orange colouration, in conjunction with the jet/shiny black, of the body.

### **Gagatopsalta obscurus** sp. nov.
(Figs 13,14,16,18-20, 41, Table 3)

Species B: Ewart & Popple, 2001, 57, 60, 61, figs 3B, 8B.

MATERIAL. HOLOTYPE; ♂, QMT99214, 1km NW Milroy Hstd. ~70 km N. Quilpie, SWQ, Light, Gidyea area, A.E(wart)., I.R(atray)., 13 Jan 2000, 26°02.28'S 144°20.43'E.

PARATYPES: SOUTHWEST QUEENSLAND: 16♂, 20♀, Dam, Milroy Hstd, ~70 km N Quilpie, gidyea, AE, IR, JN, 15.i.2000, 26°02.85'S 144°20.81'S; 4♂, 1♀, Dam, Milroy Hstd, ~70 km N Quilpie, gidyea, AE, IR, JN, 10.i.2000, 26°02.85'S 144°20.81'S; 1♂ As previously, Rec; 17♂, 7♀, Dam, Milroy Hstd, ~70 km N Quilpie, gidyea, AE, IR, JN, 11.i.2000, 26°02.85'S 144°20.81'S; 1♂, As previously, Rec; 7♂,13♀, 1 km NW Milroy Hstd, ~70 km N Quilpie, Light, gidyea area, AE, IR, 13.i.2000, 26°02.28'S 144°20.43'E; 1♂, 1♀, Milroy Hstd, ~70 km N Quilpie, Light, AE, IR, 12.i.2000, 26°02.85'S 144°20.81'E **(AE)**. 1♂, Dam, Milroy Hstd, ~70 km N Quilpie, gidyea, AE, IR, JN, 15.i.2000, 26°02.85'S 144°20.81'S; 1♀, Dam, Milroy Hstd, ~70 km N Quilpie, gidyea, AE, IR, JN, 11.i.2000, 26°02.85'S 144°20.81'S **(BMNH)**. 1♂, Dam, Milroy Hstd, ~70 km N Quilpie, gidyea, AE, IR, JN, 10.i.2000, 26°02.85'S 144°20.81'S; 1♀, Dam, Milroy Hstd, ~70 km N Quilpie, gidyea, AE, IR, JN, 15.i.2000, 26°02.85'S 144°20.81'S **(ANIC)**. 1♂, Dam, Milroy Hstd, ~70 km N Quilpie, gidyea, AE, IR, JN, 15.i.2000, 26°02.85'S 144°20.81'S; 1♀, Dam, Milroy Hstd, ~70 km N. Quilpie, gidyea, AE, IR, JN, 11.i.2000, 26°02.85'S 144°20.81'S **(MSM)**.

DIAGNOSIS. This species is very similar in appearance to *G. auranti*, the two representing sibling species. The following distinguishing characters are considered most significant: (a) The darker and more clearly defined dark median fascia present longitudinally along the abdominal sternites of *G. auranti*. (b) The more prominent broader, orange-coloured distal margin to tergite 2 in *G. obscurus*. (c) Song characteristics (see below). (d) Distribution and habitat. *G. obscurus* occurs in gidyea (*Acacia cambagei*) in southwestern Queensland, while *G. auranti* is currently known only in southeastern Queensland within brigalow and associated woodland communities.

DESCRIPTION (Male). Figs 14, 41A. *Head.* Supra-antennal plate shiny black with small median sandy-brown triangular fascia, anteriorly pointing, extending from the distal margin anteriorly to near, but not in contact with, the anterior ocellus; anterior paramedial margin adjacent to and dorsal to the bases of the antennae sandy-brown. Ocelli pink to pale red. Gena and mandibular plate shiny black with conspicuous silver pubescence. Postclypeus dominantly shiny black with minor pale brown areas between transverse ridges adjacent to dorso-lateral margin; transverse ridges shiny black. Anteclypeus shiny black with small dark brown anterior area. Compound eyes dark brown, with outer distal margin clearly separated from pronotum. Rostrum dark brown, grading to black apically. Antennae black.

*Thorax.* Pronotum shiny black with pale sandy brown central fascia not quite reaching distal or anterior pronotal margins; a pair of small paramedial pale yellow-brown reniform-like spots adjacent to the anterior margin of the pronotal collar; pronotal collar shiny black

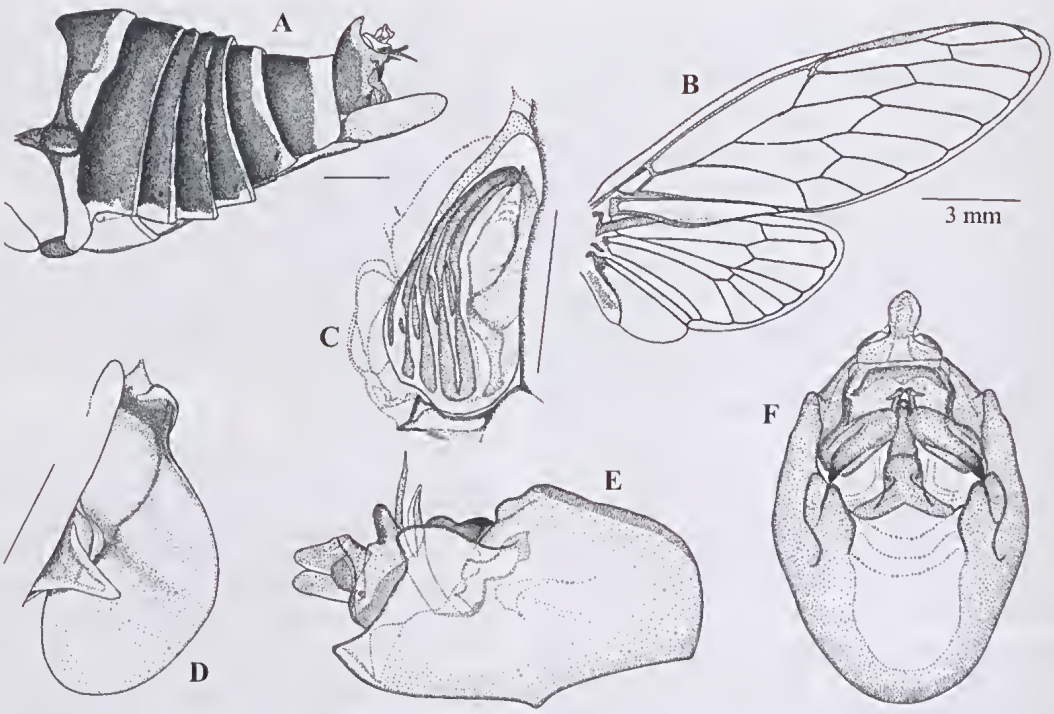


FIG. 14. *G. obscura*. A, Lateral abdomen view; B, fore and hind wings; C, timbal; the right-hand edge as shown represents the posterior margin, the top the dorsal edge; D, opereula; E, and F, lateral and ventral views of pygofer. Pygofer length 2.0mm. Seale bars = 1mm exeept wings (3mm). Drawings based on speeimens from "Milroy" H.S., approximately 70km north of Quilpie.

grading to brown at lateral corners. Mesonotum; a pair of anterior paramedial short obconical shiny black fasciae, fused medially, extending distally from pronotal collar to approximately one quarter of the mesonotum length; extending distally from these fasciae is a broad median shiny black fascia, slightly broadening distally, and terminating near the anterior area of the cruciform elevation where it coalesces with a pair of conspicuous black spots; a pair of broad black lateral fasciae extend distally from the pronotal collar, tapering and rounded distally, terminating near (but not reaching) the cruciform elevation arms; their outline is sharp, but locally crenulated; anterior margin of cruciform elevation dark brown; remaining colouration of mesonotum, including wing grooves and areas between the fasciae, is pale orange.

*Wings*. Fore wings: Costa and R+Sc veins pale orange-brown to sandy brown colour, grading to orange proximal to mesonotum; CuP vein pale orange-brown; remaining venation shiny medium to dark brown, darker apically; basal membrane orange; pterostigma with reddish infuscation, grading to brown apically and extending as a narrow marginal infuscation towards the apex of the fore wing. Hind wing with 3A vein orange, and 2A, 1A and CuP veins pale brown, remaining venation pale to dark brown, darker distally; plaga opaque white which extends along 3A vein; pale brown infuscation between plaga and adjacent anal cell.

*Legs*. Coxae shiny black on anterior and lateral edges, changing to orange on and adjacent to the trochanter and along the anterio-lateral margin of the fore coxae. Fore femora orange with three black shiny black spines, the black colour extending around and between bases of spines; mid femora with extensive lateral black to deep brown colour, elsewhere orange; hind femora dominantly orange with thin longitudinal brown fascia anteriorly. Tibiae and tarsi dominantly orange to yellow-orange, darker apically on fore legs. Claws yellow-orange with dark brown to black tips.

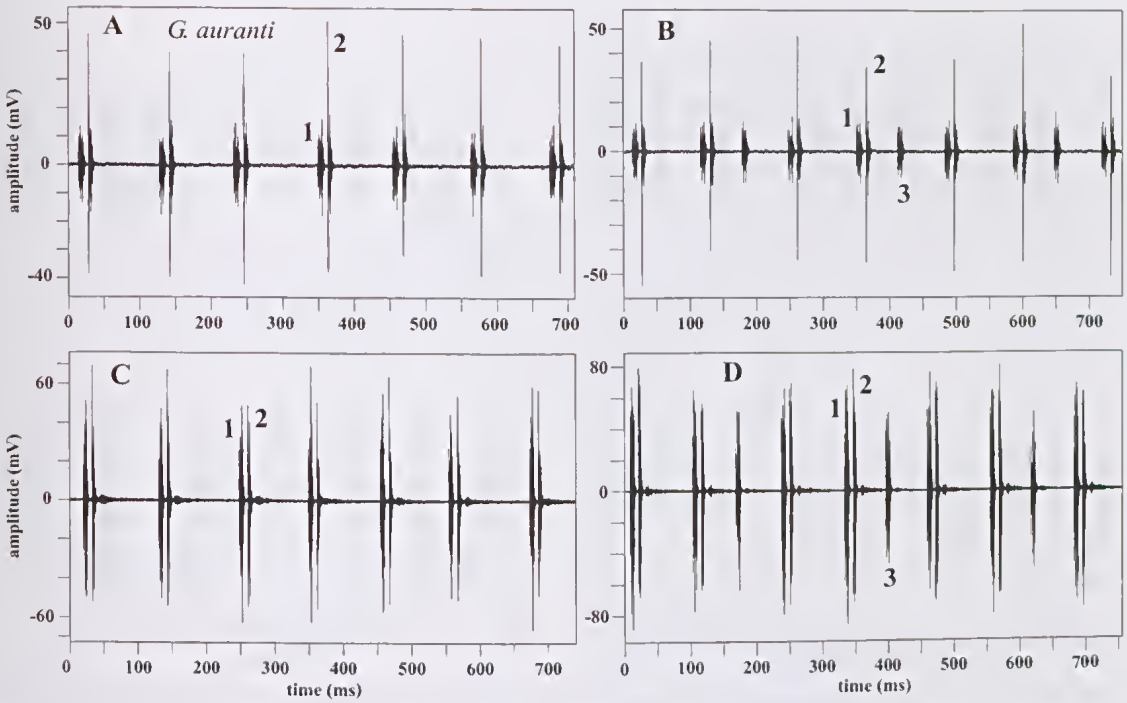


FIG. 15. Waveform plots of songs of *G. auranti* showing: (a) Regular syllable doublets (termed twin syllables; numbered 1 and 2) with no intermediate syllables; (b) the presence of regular twin syllables with alternating intermediate syllables (numbered 3); recording from specimen from Brigalow Research Station, near Theodore. In these records, the second syllable of the twin syllables has higher amplitude than syllable 1. (c) and (d) a similar sequence of twin syllables with no intermediate peak, and twin syllables with alternating intermediate syllables; recorded from Lake Broadwater, near Dalby. In these recordings, the syllables 1 and 2 are of similar amplitude. Each are unfiltered container recordings.

*Operculae*. Distal areas, extending from medial suture, pale brown; basal parts, including crest around dorso-lateral corners, vary from medium brown to black, the latter especially along the adjacent lateral margins; shapes elongated, domed and ridged, gently rounded outline extending from the lateral, through the distal to the medial margins; opercula just reach the anterior paramedial termination of sternite II, in lateral view.

*Timbals*. Ribs 3 and 4 not fused ventrally to ribs 1 and 2, but are continuous across timbal; long rib 5 extends only partially across timbal.

*Pygofer*. Refer to generic characters.

*Abdomen*. Tergites dominantly shiny black with short-sparse silver pubescence; tergite 2 with a prominent, broad orange distal margin extending completely across tergite; tergite 3 with a narrow, less conspicuous, but continuous orange distal margin; tergites 4-5 have narrow orange-brown to brown distal margins; tergites 6-7 with relatively broader pale orange-brown to medium brown distal margin; tergite 8 grades to a broad orange-brown to brown distal margin which widens laterally; ventro-lateral margins of tergites 3-7 are orange; auditory capsules predominantly shiny black, grading to dark brown centrally. Sternite II pale orange-brown, black medially; sternites III-VII orange-brown, each grading to brown distally; each exhibits the development of a diffuse, dark brown medial area, giving the overall appearance of a narrow but diffuse fascia extending longitudinally along the sternites; sternite VIII black to deep brown ventrally grading to pale brown along lateral margins.

FEMALE. Fig. 41B. General colouration shiny black and orange to orange-brown. Pronotum similar to male, but with narrow orange-brown anterior margin, and central fascia extending anteriorly to anterior margin. Mesonotum similar to male, with the black medial fascia (which

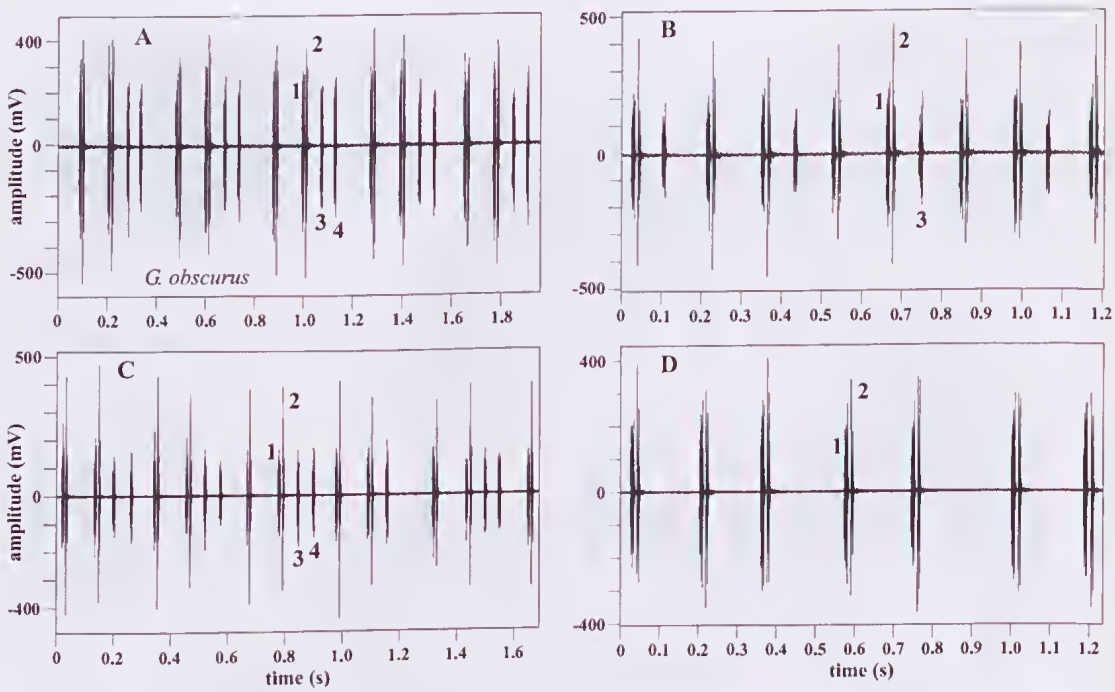


FIG. 16. Waveform plots of songs of *G. obscurus* showing: (a) twin syllables (numbered 1 and 2) with the 'normal' pair of alternating intermediate syllables (numbered 3 and 4); (b) as previously with only a single intermediate syllable (number 3); (c) twin syllables (1 and 2) with two alternating intermediate syllables (3 and 4), and in one instanee, a single intermediate syllable; (d) twin syllables with no intermediate syllables. Note the relative differenees in amplitudes between the syllables 1 and 2 in (a) to (d), and the relative timing of the intermediate syllables (3 and 4) in (a) and (c). Plots (b) and (d) superficially resemble the *G. auranti* song patterns shown in Fig. 15. Recordings from "Milroy" H.S., approximately 70km north of Quilpie, south-west Queensland, of two separate specimens. Eaeh are container recordings, filtered (FIR) to 1kHz.

extends distally from the paramedial obeonical faseiae) broadening abruptly and sharply terminating adjacent to anterior margin of erueiform elevation, whieh also exhibits a small narrow transverse black fascia. Wings and legs as in male. Tergites 3-7 similar to male, dominantly shiny black grading to deep brown laterally; tergite 2 with relatively broad continuous orange-brown distal margin, becoming progressively broader laterally; tergite 8 orange to orange-brown with narrow shiny black eolouration along anterior margin only, broadening slightly medially and laterally; tergite 9 shiny black medially, this extending as a narrow zone anterio-laterally, with a prominent black spot disto-laterally and remaining area orange to orange-brown, slightly darker along ventral margins. Sternites II-VII orange-brown grading darker brown medially, giving overall impression of a weak longitudinal faseia extending along sternites. Ovipositor sheath extends <0.5mm beyond distal margin of tergite 9.

MEASUREMENTS. N = 10♂, 10♀. *BL*: ♂ 11.2-13.4 (12.5); ♀ 11.2-13.0 (12.3). *FWL*: ♂ 14.7-16.0 (15.3); ♀ 14.7-17.0 (16.2). *HW*: ♂ 3.8-4.6 (4.2); ♀ 4.1-4.7 (4.4). *PW*: ♂ 3.5-4.1 (3.7); ♀ 3.7-4.3 (3.9). *FWL/BR*: ♂ 2.69-2.90 (2.81); ♀ 2.78-2.91 (2.83).

DISTRIBUTION & HABITAT (Fig. 13). Known so far only from the area approximately 70km north of Quilpie, southwest Queensland. In this region, it is restrieted to gidyea *(Acacia cambagei)* within the flood plain communities, oeeurring as an ineonspieuous, foliage inhabiting species. This species is encountered in small numbers from November to December (aural records), but emerges in relatively large numbers following summer rains, typically during January. The distribution of the speeies is expected to be much more extensive through south-western Queensland, in flood plain gidyea communities, than is eurrently known. It is readily eaptured at light.

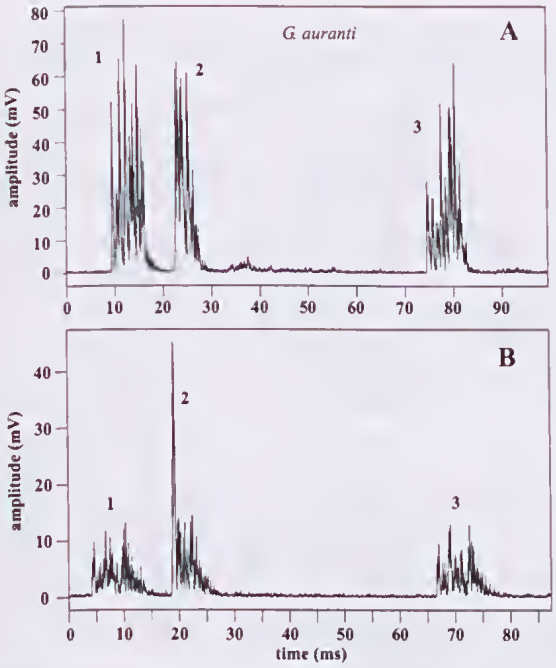


FIG. 17. Expanded time scale envelope curves of *G. auranti* songs showing detail of the twin syllables (1 and 2) and intermediate syllable (3). (a) from Lake Broadwater; (b) from Brigalow Research Station. Note the relative differences in syllable amplitudes. Other details as in Fig. 15.

ETYMOLOGY. Latin *obscurus,* inconspicuous; refers to the general habit and behaviour.

SONG. *G. auranti.* The basic song structure consists of a pair of closely spaced, but quite separate syllables (labelled 1 and 2 in Figs 15, 17) which are here together termed **twin syllables**. These repeat at intervals of 94-161ms (Table 3), the intervals slightly variable between adjacent twin syllable pairs. The intervals between syllables 1 and 2 range between 13-20ms, while the syllable lengths are 9.6-13.5ms (syllable 1), and 7.3-10.4ms (syllable 2). Relative amplitudes of the twin syllable pairs are variable (Figs 15, 17).

The major variation is the insertion of a third (labelled 3, Figs 15, 17) intermediate syllable alternately between the sets of twin syllables (1 + 2). This exerts a strong control on the intervals between each twin syllable (1 + 2), which vary between 94-128ms (no syllable 3 present) and 122-161ms (syllable 3 present). Syllable 3 has a structure and duration identical to syllable 1. The spacing of syllable 3 is asymmetric, as shown by the inter-syllable intervals of 46-69ms (i.e. between syllables 2 and 3) compared to 122-161ms between successive twin syllable pairs. Expanded envelope curves of syllables 1 and 3 (Figs 17, 19) resolve six to nine distinct hemisyllables, each with mean lengths between 0.50-0.66ms. The initial hemisyllable commonly exhibits a small but distinct separation from the immediately following hemisyllables. Syllable 2 has a structure distinct from syllables 1 and 3, comprising four to six hemisyllables, some of markedly reduced amplitude. Hemisyllable lengths range between 0.78-1.0ms, the first typically exhibiting greatest amplitude, the following syllables generally decreasing in amplitude.

Amplitude spectra (Fig. 20A) exhibit a complex series of relatively broad peaks, the maximum frequency lying between 14.8-15.0kHz, but with associated peaks at ~15.8 and 14.0-14.2kHz, and clearly defined lower frequency peaks at ~13.5, 13.0, 12.1, 10.7 and 7.7kHz. The width of the peaks, together with the concentration of dominant peaks between ~14 to 17kHz reflects the contrasting scales and

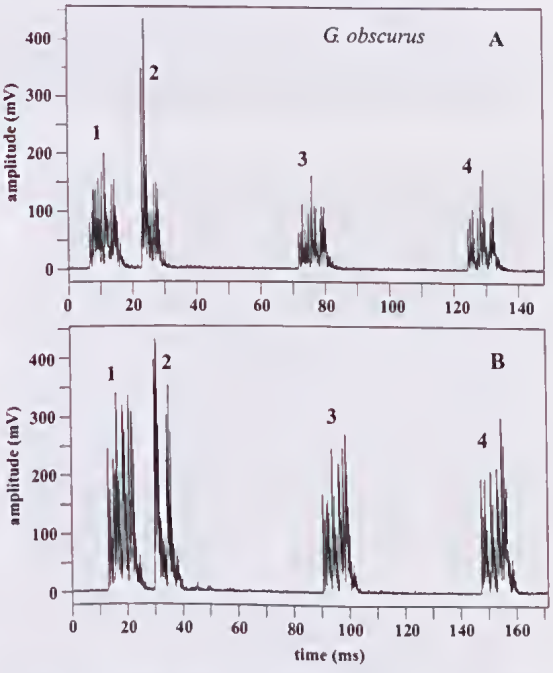


FIG. 18. Expanded time scale envelope curves of *G. obscurus* songs showing detail of the twin syllables (1 and 2) and the two intermediate syllables (3 and 4). Note the relative amplitude differences between the two separate songs. Other details as in Fig. 16.

TABLE 3. Comparison of song parameters between *G. auranti* and *G. obscurus*. [(1)]Based on data from three localities; Brigalow Research Station, near Theodore; Lake Broadwater, near Dalby; Barakula State Forest, north of Chinchilla. (2) Shown as ranges and means (in parentheses)

| | *G. auranti*[(1)] | *G. obscurus* |
|---|---|---|
| **Intervals between twin syllable sets (ms):** | | |
| (a) No intermediate syllables (4 and/or 3) present: | 97-139 (117)[(2)] | 135-281 (182)[(2)] |
| (b) Alternating intervals with intermediate syllables: | | |
| (i) Interval without intermediate syllables | 94-128 (105) | 109-143 (121) |
| (ii) Interval with syllable 3 (only) present | 122-161 (137) | 172-256 (197) |
| (iii) Interval with syllables 3 and 4 present | - | 189-284 (231) |
| **Inter-syllable intervals (ms):** | | |
| (a) Syllables 1 to 2 | 12.9-20.4 (16.0) | 16.6-17.4 (16.9) |
| (b) Syllables 2 to 3 | 46.3-69.1 (55.1) | 46.5-60.4 (54.0) |
| (c) Syllables 3 to 4 | - | 49.3-58.9 (53.5) |
| **Syllable lengths (ms):** | | |
| (a) Syllables 1 | 9.6-12.0 (11.2) | 12.5-13.5 (3.2) |
| (b) Syllables 2 | 7.3-10.4 (8.2) | 8.9-10.3 (9.8) |
| (c) Syllables 3 | 9.7-12.1 (11.1) | 11.8-15.6 (13.6) |
| (d) Syllables 4 | - | 12.1-15.1 (13.4) |
| **Inter-hemisyllable durations (syllables 1, 3 ± 4):** | 0.37-2.19 (1.18) | 0.82-2.31 (1.46) |
| **Hemisyllable lengths (excluding tails) within syllables 1, 3 ± 4 (ms):** | 0.25-0.97 (0.56) | 0.40-1.35 (0.86) |
| **Mean twin syllable (1, 2) repetition rates ($s^{-1}$):** | | |
| (a) No intermediate syllables (4 and/or 3) present | 8.5 | 5.5 |
| (b) Alternating intervals with intermediate syllables: | | |
| (i) Intervals without intermediate syllables | 9.5 | 8.3 |
| (ii) Intervals with syllable 3 (only) | 7.3 | 5.1 |
| (iii) Intervals with syllables 3 and 4 | - | 4.3 |
| **Mean frequency of dominant spectral peak (kHz):** | 14.8 | 16.6 |

variability of the component syllable and hemisyllable structures, together with the complexity of the fundamental carrier waves. The existence of the multiple spectral peaks is thought to reflect the relative importance and configuration the main sound radiation structures, as noted for the *Crotopsalta* cicadas, namely timbals, tympana and abdomen (Fonseca & Popov, 1994; Fonseca & Bennet-Clark, 1998). The complex peaks broadly centred at ~14.2-15.8kHz could represent side bands centred on the main carrier frequency at ~15kHz, i.e. amplitude modulations (~0.8kHz) with lengths of ~1.25ms. This is similar to the observed mean inter-hemisyllable lengths (syllables 1, 3) of 1.18ms (Table 3). Comparison of the spectra of individual syllables 1 and 3 indicates very similar frequency peak distributions as in the overall combined spectra (Fig. 20A), whereas individual syllable 2 spectra, although showing the similar grouping of peaks in the same maximum frequency ranges, indicate stronger development (i.e. higher amplitudes) of the lower frequency peaks between 7.5-213kHz.

*G. obscurus*. The basic song structure is close to *G. auranti*. The critical difference is the insertion of a second intermediate syllable (labelled 4, Figs 16, 18) between the twin syllable (1+2) sequences. The syllables 3 and 4 again are only inserted alternately between the twin syllable (1 + 2) sequences, which is reflected in differing intervals between the twin syllable pairs (Table 3). Aurally, the resulting song sounds remarkably similar to the 'clip-clop' of a galloping horse.

Nevertheless, during the initial stages of singing, the song commonly lacks both intermediate syllables (3 and 4), then followed by the insertion of a single intermediate syllable (3) asym- metrically and alternately between the twin syllable (1+2) pairs (Fig. 16B,D). These initial songs look superficially identical to the *G. auranti* song, but in detail, the intervals between the twin syllable pairs differ (Table 3). Nevertheless, inter-syllable intervals between

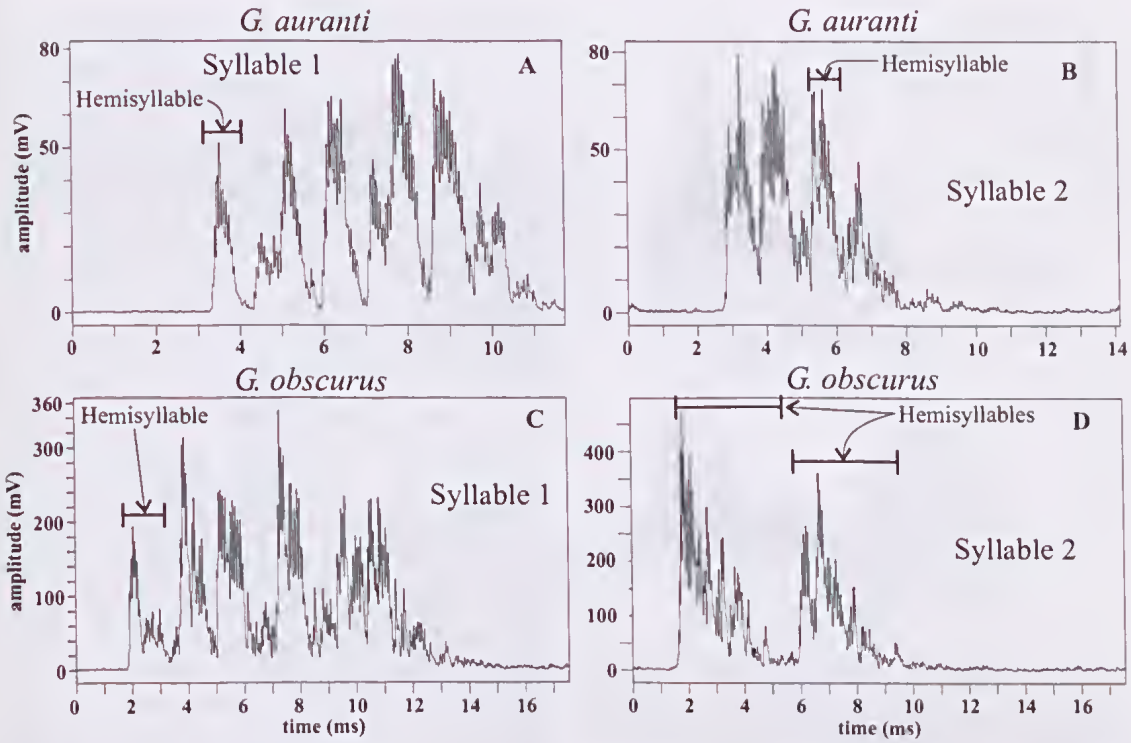


FIG. 19. Further expanded envelope curves of (a), (b), the twin syllables 1 and 2 of the *G. auranti* song showing detailed hemisyllable structures, from Lake Broadwater; (c), (d) hemisyllable structures within the twin syllables 1 and 2 of the *G. obscurus* song; recorded from "Milroy" H.S., southwest Queensland. In plots (a) to (c), only selected hemisyllables are labelled.

1-2, and 2-3, of *G. auranti* and *G. obscurus* songs completely overlap, as do the intervals between syllables 1-3. The relative amplitudes of syllables 1 and 2 are variable in *G. obscurus*, as in *G. auranti*. In *G. obscurus*, the structures and lengths of syllables 1, 3 and 4 are equivalent, but differ from syllable 2 (as in *G. auranti*).

Higher resolution expanded envelope curves of syllable 1 (Figs 18, 19; also relevant to syllables 3 and 4), reveal 5-9 distinct hemisyllables whose mean lengths range between 0.4-1.35ms. Syllable 2 is shorter than syllables 1, 3 and 4 (Table 3), consistent with *G. auranti* data, and comprises 2 clearly defined hemisyllables each ranging in total duration (including tail) of 2.5-4.3ms. In some data sets, the hemisyllable doublets of syllable 2 are complicated by superimposed shorter (higher frequency) hemisyllables ranging in length 0.8-1.7ms, comparable to those within syllables 1, 3 and 4. Amplitude spectra (Fig. 20B) are dominated by a series of complex peaks between ~15.8-17.2kHz, with broad, lower frequency peaks at ~14.9, 14.2, 13.6, 11.4-12.7, and 7.5kHz. The complexity and width of the peaks is again attributed to the variable and complex structures and lengths of the syllables and the hemisyllables. The frequency maxima feasibly incorporates two side bands centred near 16.6kHz, representing modulation rates of approximately 0.6-0.8kHz, corresponding to ~1.3-1.7ms, similar to the observed inter-hemisyllable intervals of 0.8-2.3ms. Compared to the *G. auranti* spectra, that of *G. obscurus* differs mainly in respect to the higher frequency maxima (although the potential effect of temperature differentials cannot be excluded).

Comparison of the amplitude spectra of the individual syllables 1, 3 and 4 indicate frequency peaks that are closely comparable to the spectra of the broader song pattern (Fig. 20B). Individual syllable 2 spectra exhibit similar frequency peaks, but differ in the relatively higher amplitudes of peaks in the 13.6-14.7kHz range.

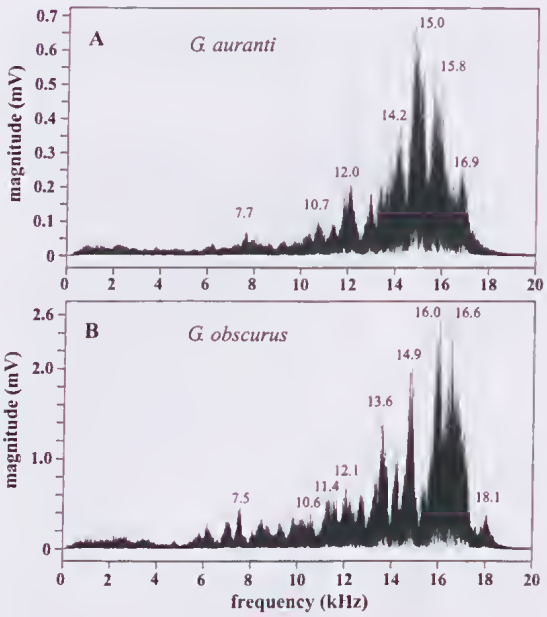


FIG. 20. Comparison of amplitude spectra of : (a) *G. auranti* song from Lake Broadwater, and (b) *G. obscurus* song from "Milroy" H.S., southwest Queensland. The frequencies of the main peaks are labelled (kHz). Both spectra based on 1.65s of song. Recordings filtered (FIR) to 0.5kHz.

The wide range of frequency seen in the spectra is similar to that of *G. auranti*, and again is thought to reflect the relative importance, efficiency and configuration of the sound radiating structures responsible for the multiplicity of frequency emission (Fonseca & Popov, 1994; Fonseca & Bennet-Clark, 1998).

Given the many similarities between the songs (and morphology) of *G. auranti and G. obscurus*, similarity between their respective timbal structures is expected (Figs 12C, 14C). The only obvious difference concerns the ventral fusion of ribs 1-3 in *G. auranti* compared to only ribs 1 and 2 in *G. obscurus*. It seems possible that the additional syllable (4) in the latter species might correlate with the difference in long rib 3 configuration, but this can only be evaluated by physiological studies.

**Caliginopsalta** gen. nov.

TYPE SPECIES. *Caliginopsalta percola* sp. nov.

INCLUDED SPECIES. *C. percola* sp. nov.

ETYMOLOGY. Latin *caligin,*dark and/or obscure, a reference to the obscure habitat and habits of the type species.

DIAGNOSIS. Small cicada, 10.5-13 mm total body length (type species). Head width including eyes greater than pronotum width across lateral margins; distance between lateral ocelli similar to distance between lateral ocellus and eyes; width of pronotum measured from lateral margins similar to width of mesonotum between fore wings; pronotal collar moderately ampliate along lateral margins and outwardly curved; abdomen tapered evenly to pygofer in dorsal view; sternites strongly rounded and clearly visible in lateral view. General colour of body pale sandy brown, brown to chestnut brown and black. Rostrum extends to anterior margins of hind coxae. Wings hyaline; fore wing with eight apical cells which are, overall, similar in length to ulnar cells (some shorter, some longer); costal vein equal in width to node with very gentle anterior curvature proximal to node; sclerotised anterior margin of costal vein narrow and less than vein width; intersection of CuA with M veins veins occurs approximately one third of distance along first vein section (proximal to basal cell) of M that makes up the inner radial cell margin;. length of the three distal vein sections that make up the inner margin of the radial cell are unequal, but not strongly so. Hind wing with six apical cells; distinctive brown infuscation fills the central area of the plaga and occurs within the anal lobe adjacent to the 3A and the 2A veins, extending to, and widening towards the distal wing margin of the 2A vein. Operculae rounded along distal and medial margins; gently domed and ridged; meracantha normal and located strongly asymmetrically within operculae towards midline; inner margins of operculae widely separated. Timbals somewhat extended anteriorly in shape; 5 long ribs, with ribs 1-4 fused ventrally; 3 prominent short ribs, plus 2 very small remnant(?) ribs between long ribs 2 and 4; dome on timbal plate narrow and laterally tapering; basal spur prominent and fused to long ribs 1-3. Pygofer: ovoid in general shape in dorsal view, but unusually broad in lateral view; upper lobe prominent with rounded termination, lower lobe small with rounded termination and no clearly defined inner lobe; prominent median process, uncal lobes curved, anteriorly pointing and sharply terminated at apices; well defined and gently curved beak; aedeagus trifid with a pair of dorsal, sclerotised

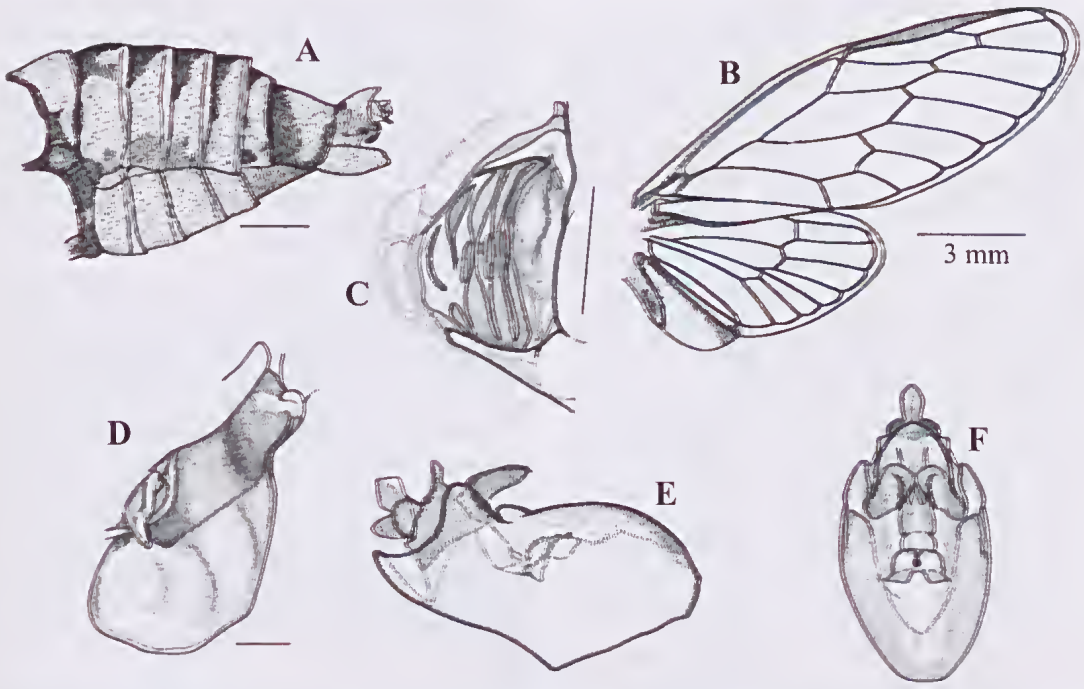


FIG. 21. *Caliginopsalta percola*. A, Lateral abdomen view; B, fore and hind wings; C, timbal; the right-hand edge as shown represents the posterior margin, the top the dorsal edge; D, opereula; E, and F, lateral and ventral views of pygofer. Pygofer length 1.8mm. Scale bars represent 1mm exeept wings (3mm). Drawings based on speeimens from the northern Barakula State Forest, north of Chinchilla.

pseudoparamers of similar length to ventral support; poorly sclerotised endotheca.

**Caliginopsalta percola** sp. nov.
(Figs 21-24, 42, Table 4)

*Notopsalta* Species D: Ewart, 1988, 183, 184, 191, 195, plate 4F; 1998, 64, 69, figs 9B, 13A.

MATERIAL. HOLOTYPE; ♂, QMT99215, Barakula S.F., nr. Chinchilla, S.Q., virgin brigalow, 15 Dec 1997, 26°14.42'S 150°48.86'E, Ewart.

PARATYPES: SOUTHEAST QUEENSLAND: 1♂, 1♀, Brigalow Res. Stn., nr. Theodore, E brigalow seetion, belah, 21.xii.2000, AE, 24°48.54'S 149°47.54'E; 1♂, Brigalow Res. Stn., nr. Theodore, E brigalow section, belah, 20.xii.2000, AE, 24°48.54'S 149°47.54'E, Rec spec 1; 1♂, As previously, Rec spec 2; 4♀, Brigalow Res. Stn., nr. Theodore, E brigalow section, belah, 20.xii.2000, AE, 24°48.54'S 149°47.54'E; 11♂, 10♀, Brigalow-belah, "Lakeview', nr. L Broadwater, via Dalby, AE, 20.xii.2001, 27°20.81'S 151°04.98'E; 7♂, 8♀, Barakula SF, nr. Chinchilla, virgin brigalow, 15.xii.1997, 26°14.42'S 150°48.86'E, AE; 1♂, As previously, Rec spec 3; 1♂, As previously, Rec spec 2; 1♂, 2♀, L Broadwater, ~30 km SW Dalby, brigalow, 20.xii.1987, JM; 2♂, L Broadwater, ~30 km SW Dalby, brigalow, 20.xii.1987, JM, (*Notopsalta* species D, Ewart 1988); 3♂, 2♀, Brigalow, L Broadwater, via Dalby, AE, 19.xii.2001, 27°20.42'S 151°05.45'E; 1♂, As previously, Rec **(AE).** 3♂, Myall Park, 8 km N. Glenmorgan, 27-28.xii.2001, Mv lamp, LWP, AS, 359-0003-006; 1♂, Myall Park, 8 km N. Glenmorgan, 27-28.xii.2001, Mv lamp, LWP, AS, On minidise, LWP, 359-0003,-0006; 1♂, 1♀, L Broadwater, via Dalby, 21.xii.1987, JM,. MV lamp, 359-0001-0002; 1♂, 27°45'S 151°13'E, 5km W Milmerran, 10.i.2004, LWP. RM; 3♂, 27°23'10"S 151°36'43"E, Jondaryan distriet, 5.ii.2005, *Casuarina cristata*, LWP, 359-00008 to 0010 **(LWP).** 1♀, 26°13'S, 150°35'E, Barakula, 23 km NNE, 18.xii.2001, GBM, DC, SW, brigalow, 400m, 10313; 8♂, 9♀, 26°04'S, 150°49'E Wonga Hills, site 3, 520m, 11.xii.2001, 10257 GBM, DC, SW, MV light, vine scrub **(QM).** 1♂, 1♀, Brigalow, L Broadwater, via Dalby, AE, 19.xii.2001, 27°20.42'S, 151°05.45'E **(BMNH).** 1♂, 1♀, Brigalow-belah, "Lakeview', nr. L Broadwater, via Dalby, AE, 20.xii.2001, 27°20.81'S, 151°04.98'E **(ANIC).** 1♂, 1♀, Brigalow-belah, "Lakeview', nr. L Broadwater, via Dalby, AE, 20.xii.2001, 27°20.81'S, 151°04.98'E **(MSM).**

DESCRIPTION (Male). Figs 21, 42A. *Head.* Supra-antennal plate pale sandy brown with irregular but continuous black colouration covering much of the central dorsal area, also enclosing each ocellus, and extending as narrow

fingers towards the anterior margin of the eyes and around the anterior postclypeal surface; a pale sandy brown, short, lanceolate fascia lies between the two posterior ocelli, extending and narrowing anteriorly towards, but not reaching the anterior ocellus; it extends distally to the pronotal margin and continues as the pronotal central fascia; a pair of small elongated ovoid castaneous areas extend obliquely from near the inner margin of the posterior ocelli towards the lateral dorsal postclypeus margin. Ocelli pink. Gena pale sandy brown with oblique black fascia lying between the eyes and mandibula plate; mandibula plate dominantly black. Postclypeus with pale brown dorso-medial area which continues to the dorsal surface, and with the pale brown anterior marginal zone of the frons; the transverse ridges and central region of frons black, the transverse ridges grading to pale sandy brown laterally. Anteclypeus pale sandy brown dorsally, black on ventral segment. Compound eyes dark brown to black. Rostrum pale sandy brown adjacent to anteclypeus, grading dark brown to black apically. Antennae dark brown.

*Thorax*. Pronotum dominantly castaneous with pale sandy brown central fascia which tapers irregularly towards, but not reaching the pronotal collar; the fascia is enclosed laterally and distally by a thin black envelope which flares outwards distally, the medial part just reaching the pronotal collar; a broadly triangular pale sandy brown area extends outwards from near the distal termination of the central fascia adjacent to the pronotal collar, narrowing and terminating paramedially; very irregular and broken black colouration occurs along, adjacent to, and between the anterior and posterior oblique fissures, further extending around the lateral pronotal margin between the posterior oblique and ambient fissures; pronotal collar, and the narrow anterior pronotal margin, are pale sandy brown. Mesonotum with a pair of black paramedial obconical fasciae, not fused medially, extending distally from anterior margin approximately a quarter of the mesonotum length; a pair of broad lateral black fasciae, very irregular and broken in form and outline, tapering distally, terminally rounded which terminate adjacent to the outer anterior margins of the anterior cruciform elevation arms; a pair of conspicuous black spots lie adjacent to the inner margins of the anterior arms of the cruciform elevation; the latter is pale yellow brown; remaining mesonotum colour and wing grooves pale sandy brown, grading to pale brown medially.

*Wings*. Costa and R+Sc veins pale sandy brown, tending translucent in costa; venation grades from pale sandy brown adjacent to basal cell to brown and dark brown apically; pterostigma with pale brown infuscation, extending slightly towards wing apex; basal membrane off-white to pale brown. Hind wing; venation pale brown grading to darker brown distally; plaga opaque offwhite, extending along both margins of 3A vein.

*Legs*. Coxae and trochanters pale sandy brown with well defined deep brown to black areas on their anterior and lateral edges. Fore femora pale sandy brown with broad longitudinal brown fasciae on outer lateral edges; three deep brown to black spines, the dark colouration extending between the bases of the spines; inner margins with more extensive brown colouration except for pale sandy brown central and dorsal areas; mid and hind femora pale sandy brown with longitudinal brown fasciae along margins. Tibiae pale sandy brown grading distally to dark brown. Tarsi and tarsal claws medium to pale brown.

*Operculae*. Relatively linear lateral margins, gently curving around distal margins, more sharply curved along medial margins; colour dominantly pale sandy brown with localised black areas adjacent to meracantha and adjacent to, but not including the crest in the distolateral corners of basal areas; gentle ridge extending distally from basal parts of operculae and narrowing towards, and terminating near distal margins. Meracantha prominent, subacutely terminated, extending above the disto-medial areas.

*Timbals*. Rib 4 discontinuous medially and rib 5 not extending completely across timbal.

*Pygofer*. Pale brown with small anterior paramedial black triangular marking, adjacent to tergite 8. See generic characters for detail.

*Abdomen*. Tergite 2 pale sandy brown to pale brown, with narrow black anterior margin extending to, and around the auditory capsules; tergites 3-7 pale sandy brown laterally, grading to pale reddish brown medially; black areas occur dorso-medially, each extended paramedially along anterior margins, tapering (somewhat irregularly) distally, and terminating at distal margins (excluding intersegmental membranes); poorly defined pale brown to brown markings occur ventro-laterally, darker on the more distal tergites, but variable between specimens; tergite 8 with black to dark brown area extending as a

narrow dorsal fascia, widening across the lateral and ventro-lateral area, the remaining area pale brown to pale reddish brown; auditory capsules black, grading to deep brown centrally. Sternite II black to deep brown; sternites III-V uniformly pale sandy brown, becoming paler brown on sternite VI; sternites VII and VIII medium to dark brown.

FEMALE. Fig. 42B. Similar markings to male with general reduction in extent of areas of black colouration. Supra-antennal plate dominantly pale sandy brown with diffuse and broken black areas around ocelli extending to lateral margin of dorsal surface of postclypeus. Postclypeus pale sandy brown; frons with central region mostly black, becoming paler dorsally; transverse ridges black medially. Gena and mandibular plate with reduced areas of black. Pronotum similar to male, but with smaller patterns of black colouration associated with the oblique fissures and lateral margin; broad central fascia pale sandy brown enclosed by brown envelope, otherwise similar to male; remaining pronotum pale brown. Mesonotum with medium to dark brown lateral fasciae, each grading black distally; their outlines similar to male, but the paramedial fasciae much reduced in size medially; the pair of spots adjacent to inner margin of anterior arms of cruciform elevation deep brown; remaining mesonotum pale sandy brown. *Wings* as in male. *Legs.* Coxae pale sandy brown each with broad wedge-shaped, deep brown to black anterior longitudinal fasciae, and narrow dark lateral dorsal edge. Femora pale sandy brown with diffuse brown longitudinal fasciae along anterior and distal edges; fore femora with three deep brown to black spines. Tibiae pale brown to pale sandy brown, darkening distally. Tarsi pale to medium brown, darker distally; claws dark brown. Tergites 2 to 9 chestnut brown medially, grading to pale brown paramedially and laterally; anterior medial areas of tergites 4-7 dark brown, grading distally to chestnut brown; distal edges and intersegmental membranes of tergites 3-7 dull yellow-brown; tergite 8 with prominent and relatively broad paramedial and lateral deep brown to black transverse fasciae, lying adjacent to tergite anterior margin; tergites 4 to 7 with very diffuse, slightly darker brown areas lying ventro-laterally; tergite 9 with a pair of broad paramedial deep brown to black fasciae extending approximately two-thirds towards distal margin of tergite, and a prominent dark spot at each disto-lateral margin. Sternites II to VI uniformly pale sandy brown; sternite VII with short dark oblique paramedial fasciae either side of ovipositor sheath entry. Ovipositor sheath extends ≤0.5 mm beyond tergite 9.

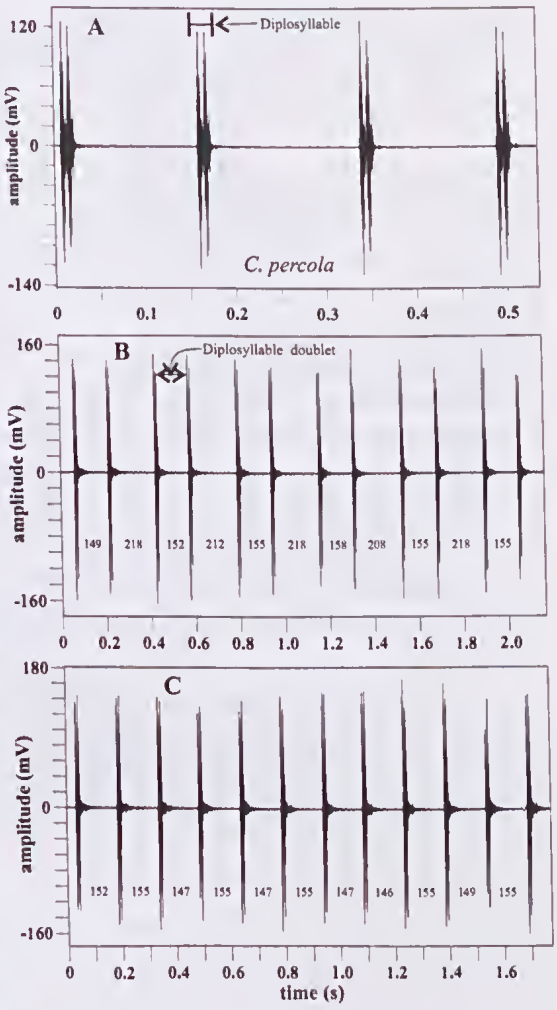


FIG. 22. Waveform plots of the *C. percola* songs. (a) Four sets of diplosyllables showing the double syllable structures; (b) the 'uneven' diplosyllable spacings with alternating short and longer inter-diplosyllable intervals, observed most commonly late in song sequences; (c) the 'even' diplosyllable spacing, in which subtle alternations of fractionally shorter and longer inter-diplosyllable intervals are still evident. The timing of the intervals is indicated in ms. Recording (a) from Brigalow Research Station, near Theodore; recordings (b) and (c) from Lake Broadwater, near Dalby. Unfiltered container recordings.

TABLE 4. *Caliginopsalta percola* -summary of song parameters from three locations. [1]Poorly defined in records from this locality. [2]These figures represent selected segments from recordings illustrating 'even' and 'uneven' intervals. The two sets of figures in each data set represent the averaged lengths of adjacent inter-diplosyllable intervals.

| | All data | Barakula State Forest | Brigalow Research Stn. | Lake Broadwater |
|---|---|---|---|---|
| **Mean diplosyllable repetition rates ($s^{-1}$, ± σ);** | | | | |
| Mean | 6.4±0.7(n=19) | 6.4±1.2 (n=6) | 6.5±0.4(n=8) | 6.2±0.5(n=4) |
| Minimum | 4.1 | 4.1 | 6.0 | 5.4 |
| Maximum | 7.7 | 7.7 | 7.1 | 6.6 |
| **Diplosyllable lengths (excluding pre-diplosyllable 'disturbance') -(ms)** | 17.0±0.85(n=8) | - | 15.9-16.6(n=4) | 17.2-18.4(n=4) |
| ***First syllable length*** (including tail) -(ms) | 8.2±0.60(n=8) | - | 7.4-7.7(n=4) | 8.5-9.0(n=4) |
| ***First syllable length*** (excluding tail) -(ms) | 4.4±0.34(n=8) | - | 4.3-4.8(n=4) | 3.8-5.0(n=4) |
| *First syllable* - | | | | |
| (i) First hemisyllable length -(ms) | 2.5±0.79(n=5) | | 2.1-2.8(n=4) | 2.0[1] (n=1) |
| (ii) Second hemisyllable length -ms | 2.0±0.75(n=5) | - | 0.65-2.4(n=4) | 2.2[1] (n=1) |
| ***Second syllable length*** (including tail) -(ms) | 8.7±0.44(n=8) | - | 8.1-8.9(n=4) | 8.3-9.3(n=4) |
| ***Second syllable length*** (excluding tail) -(ms) | 4.6±0.54(n=8) | - | 4.2-5.0(n=4) | 3.4-5.2(n=4) |
| *Second syllable* - | | | | |
| (i) First hemisyllable length - (ms) | 2.3±0.30(n=5) | - | 2.3-2.6(n=4) | 1.9[1] (n=1) |
| (ii) Second hemisyllable length -(ms) | 2.3±0.23(n=5) | - | 1.6-2.8(n=4) | 2.7[1] (n=1) |
| **Preliminary pre-diplosyllable 'disturbance'-(ms)** | 0.87±0.30(n=8) | - | 0.59-0.94(n=4) | 0.64-1.5(n=4) |
| **Inter-diplosyllable intervals -(ms)** | | | | |
| (i) 'Even' intervals (earlierin songs)[2] | -<br>- | 137±3/132±1<br>254±11/249±14 | 162±6/157±2<br>155±1/155±1 | 148±2/155±3<br>155±3/160±2<br>147±1/152±3 |
| (ii) 'Uneven' intervals (later in songs)[2] | - | 129±2/165±6<br>129±3/177±3 | 155±2/172±2 | 154±3/215±5 |

MEASUREMENTS. N = 10♂, 10♀. *BL*: ♂ 10.5-11.7 (11.1); ♀ 10.9-13.0 (12.0). *FWL*: ♂ 12.7-14.2 (13.5); ♀ 14.1-15.5 (15.0). *HW*: ♂ 3.5-3.7 (3.6); ♀ 3.7-4.1 (3.9). *PW*: ♂ 3.0-3.3 (3.2); ♀ 3.3-3.6 (3.4). *AW*: ♂ 3.2-3.4 (3.3); ♀ 3.2-3.6 (3.4). *FWL/BR*: ♂ 2.75-2.99 (2.86); ♀ 2.86-3.06 (2.94).

DISTRIBUTION & HABITAT (Fig. 13). An inconspicuous cicada restricted to both disturbed and undisturbed brigalow forest communities. It has a preference for belah (*Casuarina cristata*) within these communities, inhabiting the inner branches and foliage environments. Known locations are all in southeastern Queensland, including Jondaryan, Lake Broadwater near Dalby; the Barakula State Forest north of Chinchilla; Myall Park near Glenmorgan; near Millmerran; and the more northern area of Isla Gorge National Park and extending northwest of Theodore. The distribution is expected to occur more widely within the southern-central Queensland brigalow belt. All records are for mid to late December.

ETYMOLOGY. Latin *percol(a)*, dusky, a reference to the appearance of this species in its natural habitat.

SONG (Figs 22-24). Aurally, this consists of monotonously repeated ticks (Fig. 22A-C). In time expanded waveform plots (Fig. 22A), the 'ticks' are each resolved into discrete complex double syllables, each doublet here termed a **diplosyllable**. This term is applied as each is believed to represent an unbroken single cycle of 'in-out' buckling movements of the timbals. Diplosyllable mean repetition rates (Table 4) are similar for the three localities studied, ranging between approximately 4-8$s^{-1}$. In detail,

however, significant variability is evident. The repetition rates in fact vary from nearly even diplosyllable-diplosyllable intervals to clearly uneven intervals, the latter nevertheless exhibiting regular alternations of what are effectively 'diplosyllable doublets' (Fig. 22B; Table 4). These sequences of uneven intervals seem to occur most often towards the end of an extended song phase. The diplosyllable sequences with relatively 'even' inter-echeme intervals, however, frequently also have small, but regular variations in their alternating inter-diplosyllable intervals (Fig. 22C). Lengths of the individual diplosyllables range between 15.9 - 18.4ms.

Higher resolution envelope curves (Fig. 23A,B) reveal that each syllable comprising the diplosyllable doublets have lengths of 7.4-9.3ms (including peak tails). Each syllable is further resolved into two complex hemisyllables, best developed in the Brigalow Research Station songs (Fig. 23B), although less clearly defined in the Lake Broadwater data. The hemisyllable lengths (excluding tails) range between 1.5-2.8ms, averaging between 2.0-2.5ms (equivalent to approximately 400-500Hz). Both the syllables and hemisyllables have sharply defined initiations as well as cessations, although typically followed by a low amplitude tail. The hemisyllables comprise clearly recognisable smaller (higher frequency) pulses, considered to represent the carrier waves (Fig. 23A,B).

An unusual feature present within the diplosyllable structures is the presence of a short, low amplitude, subdued 'pre-diplosyllable disturbance' with a length of 0.59-1.5ms (equivalent to approximately 667-1695Hz). In some records (Fig.23A,B), the 'pre-diplosyllable disturbances' are themselves preceded by a very weak but distinct disturbance of the background waveform which have durations of approximately 1-1.5ms. Equivalent disturbances are not recognised preceding the second syllable within each diplosyllable. It is suggested that they may represent an initial response of the buckling of the 2 'extra' short ribs between ribs 2-3 and 3-4, noted below. The occurrence of comparable 'pre-syllable disturbances' has not been observed in the songs of any other small Queensland cicada species.

The timbals of this species (Fig.21C) exhibit the fusion of ribs 1-3 both dorsally (to basal spur) and ventrally (suggesting that they buckle in unison), while rib 4 (discontinuous medially) is fused only ventrally to ribs 1-3. Two additional

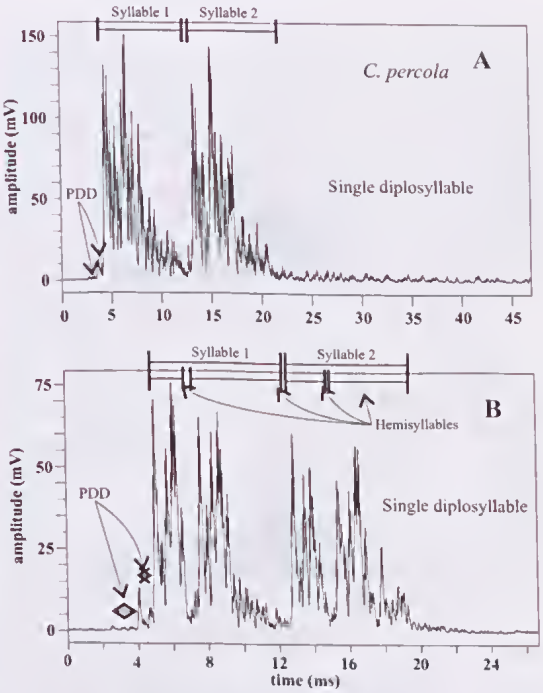


FIG. 23. Expanded time scale envelope curves showing the detailed diplosyllable and shorter hemisyllable structures, and the pre-diplosyllable 'disturbances' (PDD; arrowed) characteristics of the *C. percola* song. The higher frequency carrier pulses are clearly visible within the syllables and hemisyllables. Recording (a) from Lake Broadwater; (b) from Brigalow Research Station.

features of possible significance are the marked increase in rib width of rib 3, and the presence of a second (?relict) short rib between ribs 2-3 and 3-4 (see above). Two possible explanations for the diplosyllables seem appropriate. One is that they represent the initial inward buckling of one timbal (or both synchronously) producing syllable 1, followed by the outward buckling accompanying timbal relaxation producing syllable 2. An alternative explanation is that each syllable represents a single cycle of 'in-out' buckling of each timbal, there being a small gap in timing between the firing of the two timbals (equivalent to the inter-syllable durations, i.e. 7.4-8.9ms). This explanation implies that within each syllable, the first hemisyllable results from the inward bucking, and the second hemisyllable from the accompanying outward buckling during timbal relaxation. It is noted that within each song, there is a strong similarity of detailed structures between the two syllables comprising each diplosyllable.

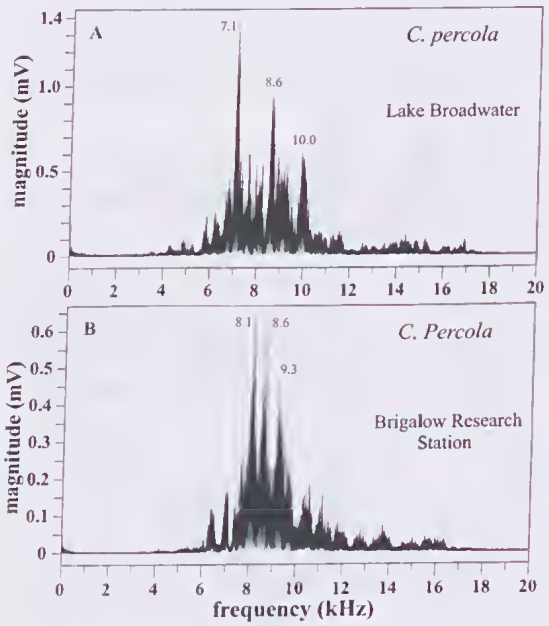


FIG. 24. Amplitude spectra of *C. percola* songs from: (a) Lake Broadwater, with bimodal (uneven) inter-diplosyllable intervals, and (b) Brigalow Research Station, with relatively even inter-diplosyllable intervals. Both spectra based on analyses of a sequence of twelve diplosyllables. The frequencies of the main peaks are labelled (kHz). Unfiltered recordings.

Amplitude spectra (Fig. 24) show the presence of broad and complex peaks centred at or near 8.6kHz, but extending between approximately 5.9 to 11.5kHz. Strongest peaks occur at 7.1, 8.6 and 10.0kHz, suggesting side bands around a 8.6kHz carrier frequency, and modulation rates of 1.4-1.5kHz, equivalent to ~0.7ms. These rates are not clearly equated to the measured syllable and hemisyllable lengths (Table 4), although they may correspond to the 'pre-diplosyllable disturbance' durations. The numerous peaks extending either side of the 8.6kHz peak suggest further side bands at approximately 0.6kHz (equivalent to a 1.7ms modulation frequency) which is similar to the lengths of the hemisyllables. The width and wide range of the frequency peaks is assumed to reflect the various diplosyllable and syllable/hemisyllable modulation rates, together with the relative roles and efficiencies of the main sound radiation structures (Fonseca & Popov 1994; Fonseca & Bennet-Clark, 1998).

## **Pipilopsalta** gen. nov.

TYPE SPECIES. *Pipilopsalta ceuthoviridis* sp. nov.

INCLUDED SPECIES. *P. ceuthoviridis* sp. nov.

ETYMOLOGY. Latin *pipil(o)*, chirp or peep; a reference to the characteristic, although soft, sharp chirping song.

DIAGNOSIS. Small cicada, 9.4-13.5 mm total body length (type species). Width of head (including eyes) only slightly greater than width of pronotum across lateral margins, but less than abdomen width (across auditory capsules); width of pronotum measured from lateral margins similar to width of mesonotum measured between fore wings; pronotal collar ampliate along lateral margins and outwardly curved; distance between lateral ocelli similar to distance between lateral ocellus and eye. Abdomen rounded to bulbous in dorsal and lateral profile, with sternites projecting well below level of tergites. Rostrum extends to midway along mid coxae. Wings hyaline without infuscations; costal vein even in width to node, with minimal curvature; sclerotised anterior costa margin weakly developed and much narrower than width of vein; fore wing with eight apical cells which are mostly shorter than length of ulnar cells; CuA-M vein intersection occurs approximately halfway along the first vein section (proximal to basal cell) of the M vein that makes up inner margin of radial cell; lengths of the three distal vein sections that comprise the inner radial cell margin are clearly of unequal length. Hind wings with six apical cells. Operculae slightly elongated, gently rounded along lateral, distal and medial margins; meracantha normal and located strongly asymmetrically (towards midline) with respect to operculae; inner margins of operculae separated but closely spaced. Timbals with five long ribs; ribs 1 and 2 fused ventrally and also anteriorly to the basal spur; three short ribs. Pygofer roughly ovate in dorsal view; upper lobe rounded and not strongly extended; lower lobe rounded and slightly enlarged; inner lobe visible, subacute; uncal lobes extend steeply from pygofer, subacutely terminated and curved anteriorly; prominent and rounded median process; beak defined but short. Aedeagus trifid, with dorsal pseudoparameres significantly longer than endotheca, and splayed outwards apically; sclerotised ventral support and partially sclerotised endotheca.

**Pipilopsalta ceuthoviridis** sp. nov.
(Figs 25-28, 43, Table 5)

Species E: Ewart & Popple, 2001, 64, 66, 71, figs 6A, 9A.

MATERIAL. HOLOTYPE; ♂, QMT99216, Cluny Lagoon, SW.Qld., 25/8/78, 24°31'S 139°37'E, A.Ewart.

PARATYPES: WEST AND SOUTHWEST QUEENSLAND: 1♂, Dam, Milroy Hstd, ~70 km N Quilpie, grass, AE, IR, JN, 13.i.2000, 26°02.85'S 144°20.81'E; 1♂, Near "Arawee", Milroy, ~70 km N Quilpie, grass, AE, 13.i.2000, 25°58.88'S 144°20.43'E; 3♂, Blackwater Ck xing, Adavale, grass, AE, IR, 15 Jan 2000, 25°54.88'S 144°36.99'E; 1♂, 3♀, Thompson R xing, 4 km W Jundah, 1.ii.1999, AE, 24°49.36'S 143°01.14'E; 1♂, Dam, Milroy Hstd,~70 km N Quilpie, grass, AE, IR, JN, 12.i.2000, 26°02.85'S 144°20.81'E, Rec; 8♂, 1♀, E segment 'Moothandella' pty, 2.1 km E Jundah Rd, 31.i.1999, AE, 25°33.85'S 143°04.24'E; 2♂, As previously, Rec; 2♂, 1♀, Warrego R xing, Charleville, 13.i.1999, AE, 26°24.04'S 146°14.05'E; 1♂, NE corner Blackall, 28.xi.1999, AE, grassland, 24°25.03'S 145°27.33'E; 1♂, NE corner Blackall, 30.xi.1999, AE, grassland, 24°25.03'S 145°27.33'E; 1♂, 10 km SW Charleville, In *Eremophila bignoniiflora*, AE, 19.x.1999, 26°26.37'S 146°09.64'E; 2♂, Warrego R. crossing, Charleville, AE, 26°24.04'S 146°14.05'E, 19.x.1999; 3♂, 1 km W Morven, 26.xi.1999, AE, 26°24.68'S 147°06.16'E; 2♂, 30.6 km S Augathella, AE, grassland, 27.xi.1999, 25°59.58'S 146°27.67'E; 2♂, 14 km NW of Tambo, grassland, AE, 27.xi.1999, 24°48.79'S 146°09.91'E, Rec; 1♂, 10 km SW Charleville, grass, AE, IR, 8.i.2000, 26°26.37'S 146°09.64'E; 1♂,~30 km N Quilpie, grass, AE, IR, 8.i.2000, 26°22.50'S 144°18.68'E; 2♂, 5.8 km W Bollon, grassland, 12.xii.2001, AE, 28°01.49'S 147°25.42'E; 1♂, 12 km S Charleville, sand plain, 8.xii.2000, AE, IR, 26°30.22'S 146°12.96'E; 1♂, Bulloo R flats, Quilpie, grassland, 11.ix.2000, AE, 26°36.77'S 144°16.78'E; 1♂, 55 km W Windorah, dune, 5.ix.2000, AE, 25°21.54'S 142°03.76'E; 1♂, As previously, Rec; 1♂, 3 km S Thargomindah, 12.ix.2000, AE, grassland, 28°00.94'S 143°50.92'E; 10♂, 1♀, Bulloo R, Milroy Hstd, nr. Adavale, 10.xii.2000, AE, IR, 26°03.42'S 144°21.23'E; 4♀, 16.5 km W Barcaldine, grassland, 12.xii.2000, AE, IR, 23°32.48'S 145°07.38'E; 7♀, 41 km SW Blackall, grass, 11.xii.2000, AE, IR, 24°41.74'S 145°17.66'E; 1♂, 0.5 km N along Muttaburra Rd., W side Thompson R, nr. Longreach, grass, AE, 16.i.2002, 23°23.67'S 144°13.21'E; 10♂, 1♀, 1 exuviae, Warrego R xing, Charleville, grass, 19.x.1998, AE, 26°24.04'S 146°14.05'E; 1♂, As previously, Rec; 1♂, 44 km SE Tambo, grass, AE, 14.i.2002, 25°10.48'S 146°29.78'E; 12♂, 1♀, Cluny Lagoon, 25.viii.1978, 24°31'S 139°37'E, AE **(AE)**. 3♂, 26°31'S, 146°04'E, Charleville, 21km SW, 4-5.iii.2003, 270m, GM, CB; 1♀, 20°49'S, 139°27'E, Mica Creek, Mt. Isa, 9-12.iii.2000, mvlamp, SE, 50277 **(QM)**. 6♂, 1♀, Red Sand hill, 55km W Windorah, 5.ix.2000, LWP, AE, 260-0001 to 0007; 1♂, Lake Houdraman, via Quilpie, 6.ix.2000, LWP, 260-0008 **(LWP)**. 1♂, Warrego R xing, Charleville, 13.i.1999, AE, 26°24.04'S 146°14.05'E; 1♂, Warrego R xing, Charleville, grass, 19.x.1998, AE, 26°24.04'S 146°14.05'E **(BMNH)**. 1♀, 41 km SW Blackall, grass, 11.xii.2000, AE, IR, 24°41.74'S 145°17.66'E **(ANIC)**. 1♂, Warrego R xing, Charleville, 13.i.1999, AE, 26°24.04'S 146°14.05'E; 1♀, 16.5 km W Barcaldine, grassland, 12.xii.2000, AE, IR, 23°32.48'S 145°07.38'E **(MSM)**. SOUTHEAST QUEENSLAND: 1♂, Jct Warrego Hwy with Jondaryan-Mt Tyson Rd, Jondaryan, grass, AE, 9.ii.2005, 27°22.88'S 151°36.75'E, field rec **(AE)**. 3♂, 27°22'34"S 151°36'00"E, Jondaryan district, grass, 5.ii.2005, LWP, 360-0009 to 0011 **(LWP)**. SOUTH AUSTRALIA: 1♂, 27.54'S 135.49'E, Neales R, 22viii.1989, l. Bunic **(ANIC)**.

DESCRIPTION (Male). Figs 25, 43A. General colouration most commonly bright apple green; rarer pale brown, pale yellow-brown, pale mauve and yellow-green specimens occur. The following description is based on the normal green form.

*Head.* Supra-antennal plate, postelypeus and transverse ridges, gena, mandibular plate and anteelypeus all bright apple green. Ocelli pink to pale red. Compound eyes medium to red-brown. Antennae fawn to pale brown. Rostrum pale sandy brown, grading darker apically.

*Thorax.* Pronotum bright apple green, including anterior margin, pronotal collar and central fascia area; variation in intensity of colour, tending towards a more translucent appearance between and along the oblique fissures. Mesonotum with a pair of wide pale grey-brown obconical paramedial fasciae which extend and taper distally from anterior margin about one quarter of the distance along mesonotum, but not quite fused anteriorly; a pair of pale grey-brown broad lateral fasciae, irregular and broken in outline, extend and taper distally from anterior margin to near anterior arms of cruciform elevation; remaining colour apple green to pale yellow-green, with pale sandy colour along wing grooves.

*Wings.* Fore wing venation pale green, basal membrane pale sandy yellow. Hind wing with pale green venation; plaga pale sandy yellow which extends along both margins of 3A vein.

*Legs.* Dominantly pale green with diffuse pale sandy yellow areas (possibly due to fading in storage) on anterior margins of coxae and trochanters, and as weakly developed longitudinal fasciae on femora. Tibiae tending pale brown distally. Tarsi pale greenish brown, with apices of claws brown.

*Operculae.* Pale green; distal margins gently curved, but becoming more sharply curved along medial margins; gentle short doming developed

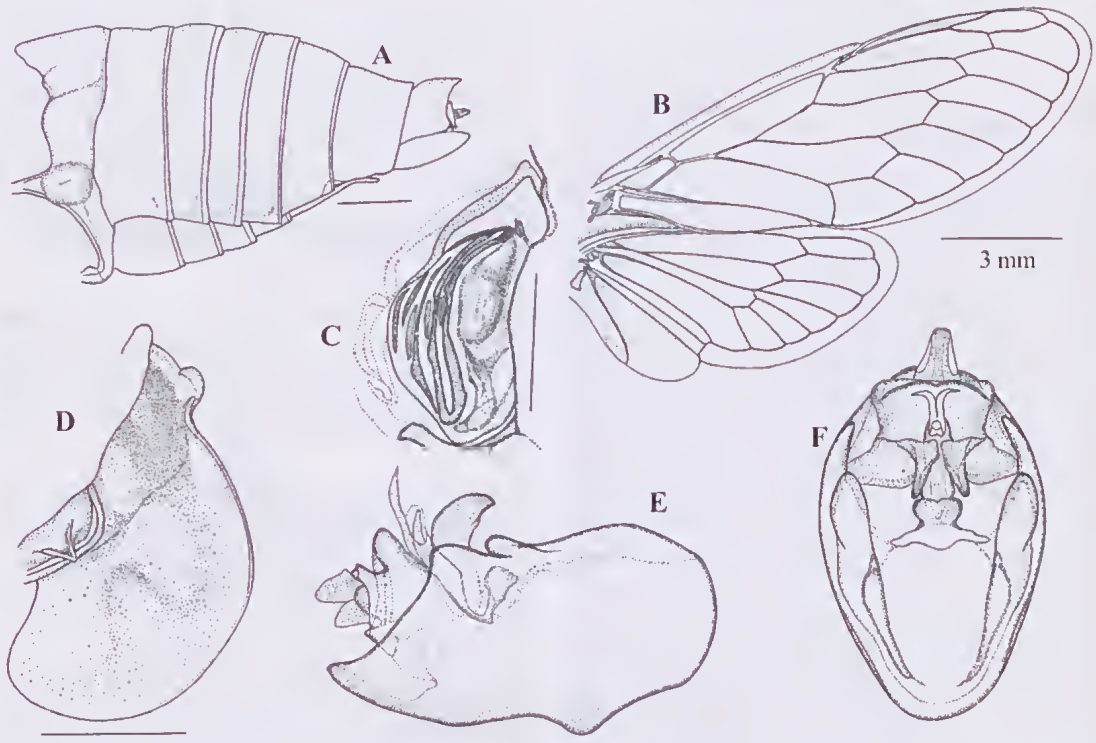


FIG. 25. *Pipilopsalta ceuthoviridis*. A, Lateral abdomen view; B, fore and hind wings; C, timbal; the right-hand edge as shown represents the posterior margin, the top the dorsal edge; D, opercula; E, and F, lateral and ventral views of pygofer. Pygofer length 1.7mm. Scale bars represent 1mm except wings (3mm). Drawings based on specimens from Cluny H.S. lagoon, near Bedourie, and "Milroy" H.S. north of Quilpie (pygofer only).

from distolateral areas extending to basal areas; meracantha small, subacutely terminated

*Timbals*. Rib 3 extends across timbal, while ribs 4 and 5 are relatively short; in some specimens, rib 5 apparently exhibits a remnant small discontinuous extension ventrally; ribs 3 to 5 not fused to basal spur; well developed, but relatively small central dome on timbal plate.

*Abdomen*. Tergites bright apple green, without any clearly defined fasciae. Sternites apple green, tending towards yellow-green distally.

*Pygofer*. Apple green, becoming darker towards beak. Details as in generic characters.

FEMALE. Fig. 43B. Dominantly uniform apple green, similar overall to male. Antennae dark brown apically. Ocelli pale pink. Compound eyes dark brown to red-brown. Postclypeus with medial segments between the transverse ridges dark brown to black, these coalescing dorsally; in some specimens, there is minor black mottling dorsally on postclypeus and supra-antennal plate. Legs usually as in male, but sparse thin dark brown fasciae are seen on the fore tibiae, mid and hind femora, and fore trochanters of some specimens. Ovipositor black on apex; ovipositor sheath extends approximately 1 to 1.3 mm beyond tergite 9.

MEASUREMENTS. N = 11♂, 11♀. *BL*: ♂ 9.4-13.5 (12.0); ♀ 10.7-13.0 (11.9). *FWL*: ♂ 9.7-13.0 (12.2); ♀ 12.2-13.7 (12.8). *HW*: ♂ 2.6-3.8 (3.2); ♀ 2.8-3.3 (3.0). *PW*: ♂ 2.5-4.0 (3.4); ♀ 3.0-3.6 (3.3). *AW*: ♂ 3.0-4.4 (4.0); ♀ 3.3-3.7 (3.5). *FWL/BR*: ♂ 2.50-2.88 (2.64); ♀ 2.48-2.81 (2.63).

DISTRIBUTION & HABITAT (Fig.13). A relatively localised, highly cryptic and static species inhabiting the low grasslands of predominantly inland Queensland, including the Mitchell grass plains. It sits in short to moderately short grass, typically singing in full sunshine. The known distribution extends to

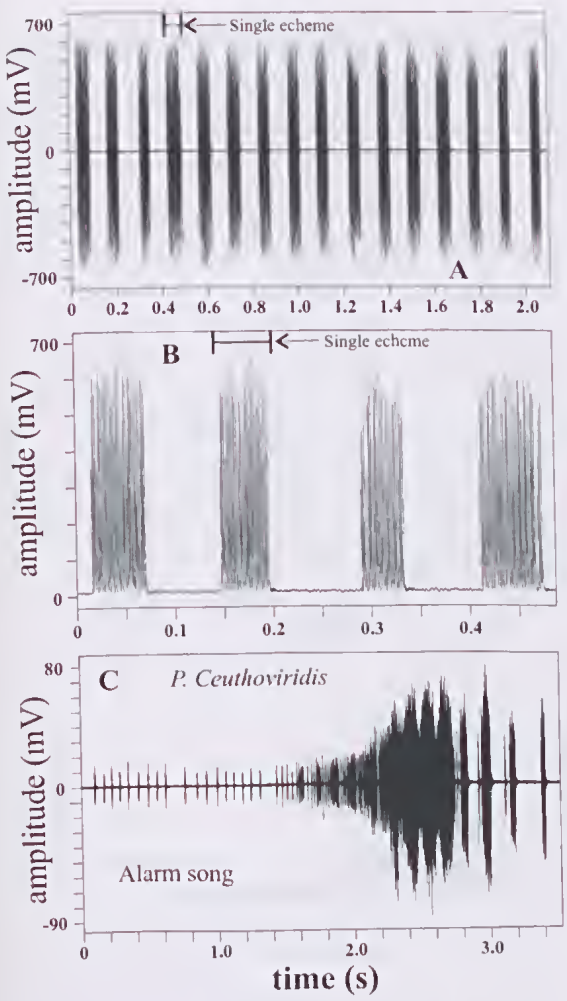


FIG. 26. *P. ceuthoviridis*. Waveform plots of; (a), (b) normal chirping song comprising repetitive, sharply defined echemes, and (c), alarm song when under stress. In (b), a time expanded envelope plot shows the multiple syllables comprising each echeme. Data in (a) and (b) based on field recordings, unfiltered, from 55km west of Windorah; (c) represents a container recording, unfiltered, from 44km southeast of Tambo.

northern South Australia, but it is almost certainly a widespread species throughout the inland regions of Australia. Known Queensland localities extend west and southwest of Bollon and Morven, including Charleville, Thargomindah and westwards to Quilpie, Adavale, Windorah, Jundah and Cluny H.S. (near Bedourie). Northern inland locations include Augathella, Tambo, Blackall, Barcaldine and the Longreach region, plus a single more northern record from Mica Creek at Mt. Isa. An isolated record exists from southeastern Queensland at Jondaryan. The South Australian record is from Neales River (Creek).

ETYMOLOGY. Greek *ceutho,* and Latin *viridi(s);* referring to the hidden/concealed habits and behaviour and to the bright apple green colouration typical of this species, respectively.

SONG (Figs 26-28). Data are based on recordings from six southwestern Queensland locations, namely: 55 km W. of Windorah; Moothandella H.S. (nr. Windorah); Cluny H.S. (near Bedourie); Charleville; Tambo; and Milroy H.S. (70 km N.Quilpie), plus a recording from Jondaryan in southeastern Queensland. Four data sets are presented in detail (Table 5).

The song consists of monotonously repeated sequences of nearly identical (within a given song cycle) short echemes ('chirps'), ranging

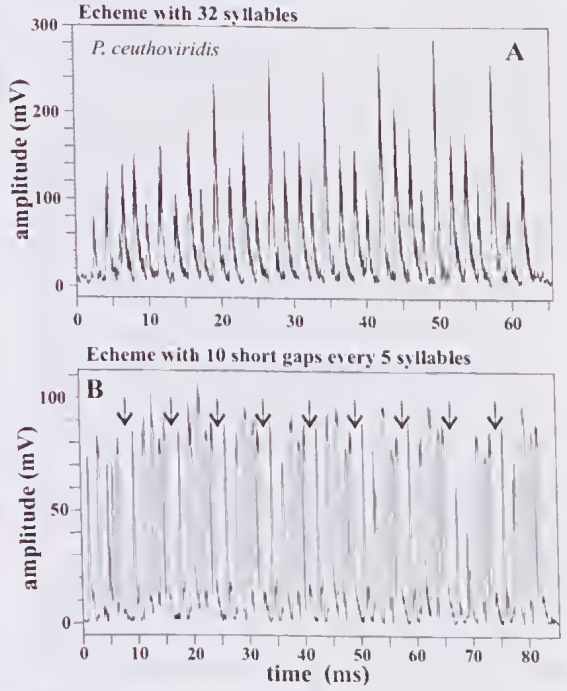


FIG. 27. Expanded time scale envelope plots of single echemes in *P. ceuthoviridis* songs showing the individual syllables; (a) from the Warrego River at Charleville, southwest Queensland; (b) Jondaryan, southeast Queensland. In (b), small short time gaps between the sets of five syllables are arrowed. Unfiltered field recordings.

TABLE 5. *Pipilopsalta ceuthoviridis* - summary of song parameters, based on field recordings from four locations. [(1)]Based on separate wave form plots from seven separate locations. [(2)]Figures represent mean values,±σ, number of measurements (n), and measured ranges of data (in brackets). [(3)]Figures represent mean values, equivalent inter-echeme intervals in ms [in brackets], and measured ranges of data (in brackets). [(4)] Based on mean frequencies of dominant spectral peaks of each recording, and mean value of the measured mean frequencies.

| | All data | Cluny | Charleville | W. Windorah | Jondaryan |
|---|---|---|---|---|---|
| | | | | | |
| **Inter-echeme intervals - ms** | 141[(1)] | 160±5(n=11) (150-165)[(2)] | 117±4(n=15) (110-124)[(2)] | 137±11 (n=30) (122-153)[(2)] | 148±4(n=55) (137-156)[(2)] |
| **Echeme lengths - ms** | 68.1[(1)] | 74.0±8.0(n=14) (60.2-85.0)[(2)] | 64.9±4.5(n=19) (55.5-71.2)[(2)] | 49.3±9.7 (n=20) (27.4-63.7)[(2)] | 84.1±6.0(n=60) (68.0-95.0)[(2)] |
| **No. of syllables per echeme** | 40.1[(1)] | 44.4±4.8(n=14) (36-51)[(2)] | 34.4±2.5(n=19) (30-66)[(2)] | 31.2±6.1 (n=20) (17-40)[(2)] | 50.4±4.3(n=60) (40-58)[(2)] |
| **Syllable lengths (including. tail) - ms** | 1.68 | 1.64±0.54(n=60) (0.56-2.68) | 1.88±0.18(n=39) (1.52-2.28) | 1.58±0.31 (n=79) (1.06-2.85) | 1.63±0.47(n=122) (0.52-2.85) |
| **Hemisyllable lengths - ms** | 0.53 | 0.50±0.18(n=27) | 0.68±0.02(n=2) | 0.54±0.08 (n=8) | 0.41±0.11 |
| **Echeme repetition rates ($s^{-1}$); measured from multiple echeme counts** | | | | | |
| (i) Field | 7.34±0.89 (n=13) | 6.29[159] (6.19-6.39)[(3)] | 8.62[116] (8.57-8.68)[(3)] | 7.71[130] (7.44-8.11)[(3)] | 6.76[148] (6.72-6.83)[(3)] |
| (ii) Container | 6.85±0.90 (n=8) | | | | |
| **Maximum frequency - Mean (kHz)[(4)]** | 15.4 | 15.1 | 15.5 | 14.8 | 15.4 |
| **Mean frequency - (kHz)[(4)]** | 15.1 | 15.0 | 15.2 | 14.6 | 15.2 |

between 27-95ms in length. The term echeme is used on the basis of the presence of trains of multiple syllables without significant gaps, which are thought to represent more than a single cycle of the buckling of the timbal pairs. Inter-echeme intervals range between 110-165ms (Fig. 26), equating to repetition rates of approximately 6 to 9$s^{-1}$. Comparison of these rates between field and container recordings indicate little significant difference (Table 5), although container recordings tend to be slightly slower. Each echeme consists of coalescing syllables (Figs 26b, 27) 17- 66 in number, their overall structures being similar throughout each echeme, i.e. there being no systematic temporal or peak amplitude variations. In some recordings from N.W. Windorah, Cluny and Jondaryan, there exists an indication of regular groupings or sets of five syllables within the echemes, each group separated by slightly increased inter-syllable gaps (Fig. 27b). It seems possible that each syllable grouping represent a single contraction (and relaxation?) cycle of one timbal. The sequential alternation of the timbal pairs would, in this explanation, provide the unbroken trains of syllables seen in each echeme.

Higher resolution envelope curves of the syllables (two separate records shown in Fig. 28A, B) show each to have a sharply defined initiation and decay to and from their maximum amplitudes, followed by either a low amplitude tail, or commonly by low amplitude secondary peaks (termed hemisyllables). Mean measured syllable lengths (including tails, i.e. peak to peak) range 1.58-1.88ms (equivalent to modulation rates of 532-633Hz). The mean lengths of the individual hemisyllables range between 0.41-0.68ms (Table 5). The hemisyllables vary in their exact temporal relationships to the syllables. A possible explanation for their production is that they represent the clicks emitted during relaxation of the timbal ribs following primary syllable production.

Comparison of the song parameters between the songs of the two most geographically separated recordings ( Table 5) shows the essential similarity and stability of the song

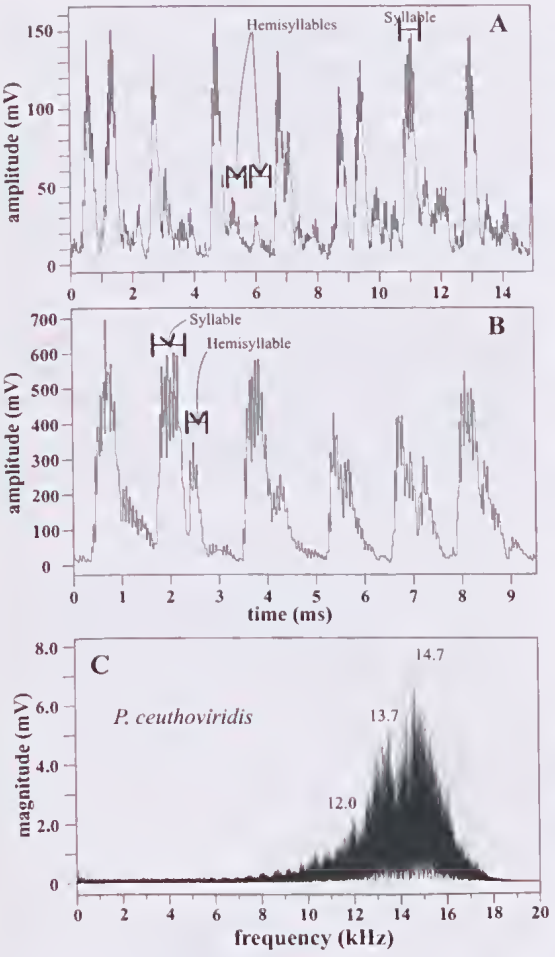


FIG. 28. (a) Detailed syllable and lower amplitude hemisyllable structures within a short time segment of an ecbeme, showing uneven inter-syllable intervals; recorded from Cluny H.S. lagoon; (b) as previously, based on recorded specimen from 55km west of Windorah. In these two plots, only selected syllables and hemisyllables are labelled; (c) amplitude spectrum of *P. ceuthoviridis* song from 55km west of Windorah. Main frequency peaks are labelled (kHz). All are unfiltered field recordings.

structures, even though separated by a linear distance of about 1240km.

Amplitude spectra (Fig. 28C) show the spectra to possess a complex broad peak centred at 14.7kHz, but extending between ~12 to 17kHz. There are very subdued peripheral peaks at ~10.4, 12, 12.5 and 16.2kHz. No significant sidebands peaks can be clearly identified. The width and complexity of the dominant peaks are nevertheless attributed, at least in part, to the complex, overlapping ranges of lower frequency side band peaks which reflect the range of amplitude modulation structures seen within the echemes, syllables and hemisyllables. The carrier frequency is inferred to correspond to the main peak maxima at 14.7kHz. The absence of peaks extending to lower frequencies, as seen in the other species described in this paper, suggest either that sound radiation was concentrated in a smaller number of body structures, or that these structures are perhaps more coherently tuned. It is therefore perhaps significant to recall that *P. ceuthoviridis* is a localised and relatively static species.

Timbal structure has five long ribs and three short ribs. Only ribs 1 and 2 are fused ventrally and dorsally (to basal spur), the remaining long ribs lying 'suspended' on the timbal resilin. It is possible that ribs 1 and 2 are partially or even completely coupled, and react independently from ribs 3-5, giving rise to the complexities seen in the detailed syllable structures. The groupings of 5 syllables seen within some echemes, noted above, may correlate with the buckling of each long rib within a single timbal buckling cycle.

The stress call (Fig. 26C) of this species is very different from the calling song, and contains significantly more complex temporal and amplitude modulations. The maximum frequency however, is 14.9kHz, close to the calling song maximum.

## **Drymopsalta** gen. nov.

TYPE SPECIES. *Drymopsalta crepitum* sp. nov.

INCLUDED SPECIES. *D. daemeli* (Distant, 1905), n.comb.; *D. crepitum* sp. nov.

ETYMOLOGY. Greek *drymo,* wood/woodland; a reference to the habitat preference.

DIAGNOSIS. Small cicadas, <15 mm total body length. Width of head (including eyes) greater than width of pronotum across lateral margin, the latter similar to the abdomen width across the auditory capsules; width of pronotum measured from lateral margins similar to, or slightly greater than mesonotum width measured between fore wings; pronotal collar moderately to strongly ampliate along lateral margin and outwardly curved; distance between lateral ocelli similar to distance between lateral ocellus and eye. Abdomen slender and evenly tapered distally; sternites rounded and visible when viewed

laterally, although sternites VI and VII may only just be visible. Rostrum extends beyond the hind coxae. Wings hyaline and relatively elongated; forewings with costal vein more or less equal in length to node and exhibits a marked anterior curvature proximal to node; sclerotised area along anterior margin of costal vein very narrow; fore wing with eight apical cells which are similar, overall, to length of ulnar cells (some longer, some shorter); intersection of M and CuA veins occurs approximately one half of distance along first vein section (proximal to basal cell) of M vein that makes up inner margin of radial cell; lengths of the three distal vein sections that make up inner margin of radial cell are clearly of unequal length. Hind wing with normally 5 to 6 apical cells, rarely 4; these vary not only between species, but sometimes are variable within a single specimen. Operculae elongated with somewhat blunt, oblique and variably rounded distal margins; meracantha normal and located strongly asymmetrically, towards midline, relative to operculae; inner margins of each opercula widely separated. Timbal with four to five long ridges, ribs 1-3 always fused ventrally; ribs 1-4 fused anteriorly with the clearly developed basal spur; three short ribs, sometimes very weakly developed. Pygofer ovoid to roughly rectangular-shaped in dorsal view; upper lobes moderately extended, subacute, but apically rounded; lower lobes well developed, apically rounded; inner lobes not developed; uncal lobes erect, extending almost orthogonally, and thickened and rounded apically; conspicuous beak; median process small and narrow in lateral view; aedeagus trifid with dorsal pseudo

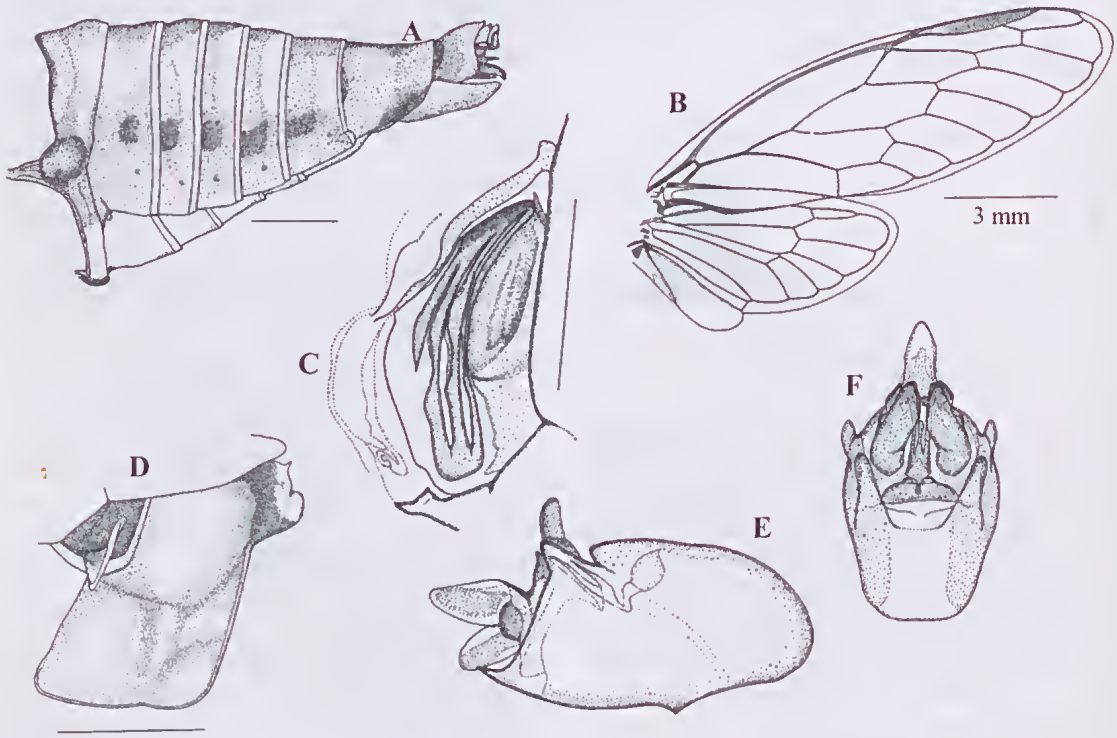


FIG. 29. *Drymopsalta crepitum*. A, Lateral abdomen view; B, fore and hind wings; C, timbal; the right-hand edge as shown represents the posterior margin, the top the dorsal edge; D, opercula; E, and F, lateral and ventral views of pygofer. Pygofer length 1.5mm. Scale bars represent 1mm except wings (3mm). Drawings based on specimens from Heathlands H.S., and Cockatoo Creek, near Heathlands Resource Reserve (pygofer only), northern Cape York Peninsula.

parameres longer than endotheca, sclerotised ventral support, and unsclerotised endotheca.

**Drymopsalta crepitum** sp. nov.
(Figs 29-35, 44)

Species F: Ewart, 1993, pp. 139, 147, fig. 14 (not fig. 12 as labelled); Heathlands species F: Ewart, 2005, p.172, fig 5.

MATERIAL. HOLOTYPE; ♂, QMT99217, Pumphouse, Heathlands Stn., Cape York Peninsula, N.Q., 1 Feb 1992, A. Ewart, 11°45.35'S 142°35.38'E.

PARATYPES: CAPE YORK PENINSULAR, QUEENSLAND: 2♂, 4♀, Pumphouse, Heathlands Stn, 16.i.1992, AE, 11°45.35'S 142°35.38'E; 4♂, As previously, 21.i.1992; 6♂, 4♀, As previously, 25.i.1992; 7♂, 5♀, As previously, 1.ii.1992; 2♂, 1♀, Open Forest, nr. Heathlands Stn, 26.i.1992, AE, 11°45.24'S 142°34.62'E; 4♂, 4♀, Nr. Cockatoo Ck xing, ~18 km NW Heathlands Stn, 20.i.1992, AE, 11°39.19'S 142°27.36'E; 2♂, 2♀, Nr. Bertie Ck xing, ~12 km SW Heathlands Stn, 19.i.1992, AE, 11°49.70'S 142°29.89'E; 1♂, 3♀, Heathlands Stn, 24.i.1992, AE, 11°45.11'S 142°34.34'E; 1♂, Nr. Cockatoo Ck xing, ~18 km NW Heathlands Stn, 31.i.1992, 11°39.19'S 142°27.36'E; 1♂, Tall heath, N side Pennefather R, 2.xi.2002, AE, 12°13.45'S 141°45.41'E, Rec spec 1; 1♂, As previously, Rec spec 2; 2♂, Tall heath, N side Pennefather R, 3.xi.2002, AE, 12°13.45'S 141°45.41'E; 1♂, As previously, Rec spec 3; 1♂, 1♀, Tall heath, N side Pennefather R, 5.xi.2002, AE, 12°13.45'S 141°45.41'E; 1♂, As previously, anomalous song type; 1♂, ~0.7km S of Base Camp, Pennefather R, S side of entrance, heath, 7.xi.2002, AE, 12°14.60'S 141°42.89'E; 34♂, 10♀, 10.8 km N of Norman R, Normanton, mixed *melaleuca* woodland, AE, 14.i.2003, 17°37.10'S 141°09.17'E; 1♂, As previously, Rec spec 1; 1♂, As previously, Rec spec 2 **(AE).** 1♀, Cape Flattery heath, 45km N Cooktown 13-14 July 1976, GB&SRM **(QM).** 1♂, Browns Ck, W of Tozer Gap, 9.i.1988, AW-H; 12♂?, 7♀, Tozer Gap, Iron Range, 27.xii.1983, MS&BJM; 1♀?, Jardine R xing, 11°09'S 142°22'E, 11.x.1979, MS&BJM; 3♂, 1♀?, Jardine R xing, 11°09'S 142°22'E, 29.x.1979, MS&BJM; 3♂?, 2♀, Dalhunty R xing, N of Coen, 2.xii.1983, AW-H; 1♂?, 1♀, Gunshot Ck, 11°43'S 142°29'E, 21.iii.1992, GD, SM; 1♂, Punsand Bay, 16.i.1987, RBL; 1♂, 1♀, Archer R., April 1988, SL **(MSM).** 13♂, 4♀, Gunshot Ck., 13 km NW Heathlands HS, 11°43'S 141°28'E, 21.iii.1992, mv lamp, GD, MAS; 1♂, Iron Ra, West Claudie R, open forest, 3.xii.1985, DY **(UQIC).** 1♂, Nr. Cockatoo Ck xing, ~18 km NW Heathlands Stn, 20.i.1992, AE, 11°39.19'S 142°27.36'E; 1♀, Pumphouse, Heathlands Stn, 16.i.1992, AE, 11°45.35'S 142°35.38'E **(BMNH).** 1♂, 1♀, Pumphouse, Heathlands Stn, 1.ii.1992, AE, 11°45.35'S 142°35.38'E **(ANIC).**

DESCRIPTION (Male). Figs 29, 44A. General colouration pale to medium brown and black.

*Head.* Brown to black with fine silver pubescence. Supra-antennal plate medium brown with short yellow fascia extending along medial suture from distal margin to between the two posterior ocelli; irregular black patches enclosing ocelli. Gena brown; mandibular plate brown with narrow black margin adjacent to anteclypeus; prominent silver pubescence. Postclypeus dominantly black to dark brown dorsally with median pale yellow-brown fascia extending anteriorly to dorsal anterior margin; frons pale sandy colour with black transverse ridges which become paler laterally. Anteclypeus pale brown with small median darker spot. Compound eyes pale brown. Ocelli pink to pale red. Rostrum pale sandy brown, darker brown apically. Antennae dark brown, grading pale brown apically.

*Thorax.* General colour pale brown to black. Pronotum with black central fascia, slightly broadened adjacent to both the distal and proximal margins, appearing somewhat 'dumbell'-shaped, and enclosed by a medium brown envelope without pubescence; between the anterior and posterior oblique fissures occur areas of both broken and continuous black colouration; the posterior oblique fissure is also marked by broken black colouration; short thin irregular black fasciae lie proximally to the lateral margin; anterior pronotal margin and pronotal collar are pale sandy-yellow except for localised black colouration at outer corners of collar. Mesonotum with a pair of anterior, paramedial, short broad black obconical fasciae, tapered distally, just coalescing adjacent to pronotal collar, and extending distally approximately one quarter of the distance along the mesonotum; a pair of broad lateral fasciae, brown to black colour, tapered distally and enclosed by medium brown colouration; two small elliptical black spots located anteriorly to the anterior arms of cruciform elevation; remainder of mesonotum colour medially is pale-medium brown, paramedially sandy brown, and laterally pale brown; cruciform elevation pale sandy brown on anterior arms and in lateral area between arms, remainder deep brown to black; wing grooves pale sandy brown; scattered silver pubescence.

*Wings.* Fore wing venation medium brown, with costal vein colourless to translucent; pterostigma infuscated reddish to dark brown; basal membrane opaque white. Hind wing venation pale brown; 5 apical cells, very rarely 4; plaga opaque white which extends along both sides of 3A vein.

*Legs.* Coxae pale sandy brown; fore coxae dark brown on distal lateral margins; mid and hind

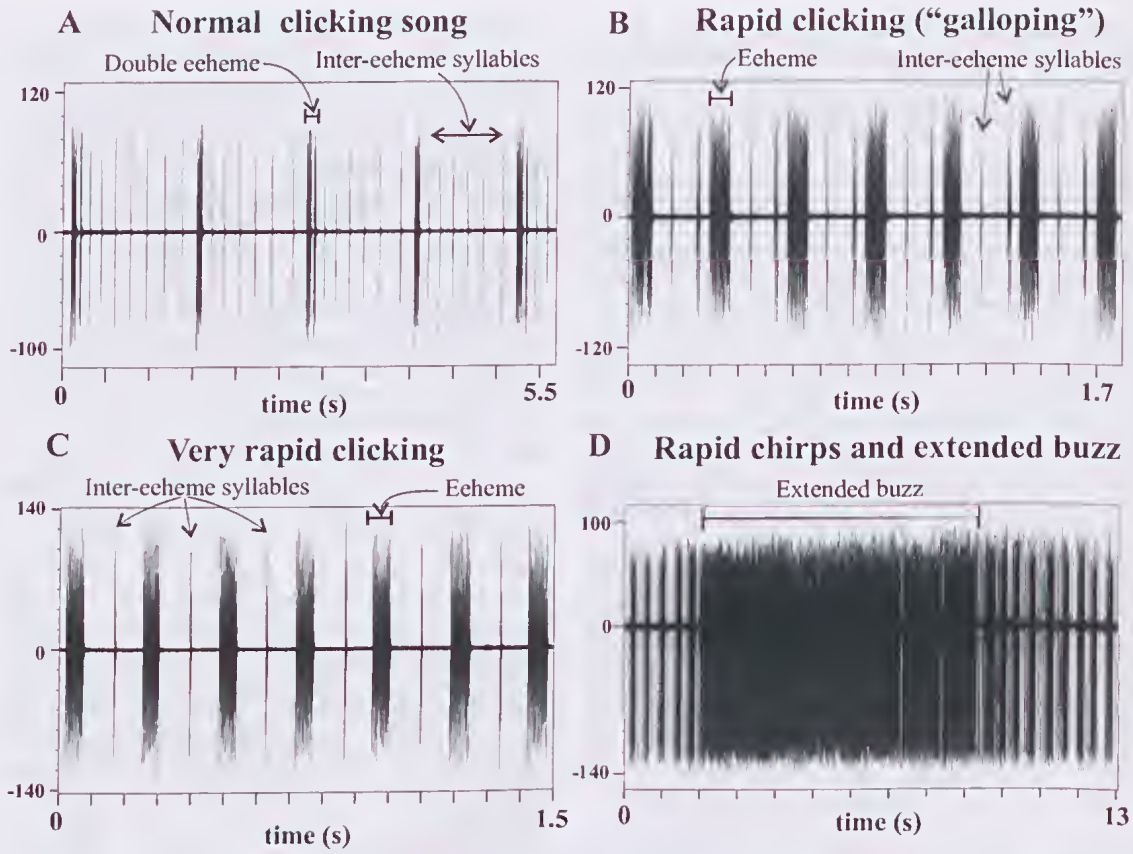


FIG. 30. Waveform plots of four described phases of the *D. crepitum* songs. The change from the normal song (a), through to the buzzing phase (d) is gradational. Plots (a) and (d) recorded from the northern shores of the Pennefather River, northwestern Cape York Peninsula. Only selected eehemes, double eeheme, and inter-eeheme syllables are labelled. Plots (b) and (c) recorded from 11km north of Normanton, northern Queensland. Recordings (a) to (c) were made in a container, filtered (FIR) to 1kHz, while (d) represents a bat detector field recording.

coxae with broad dark brown fasciae along anterior margins. Fore femora with alternate pale sandy brown and medium brown longitudinal fasciae, and three dark brown spines; mid and hind femora dominantly medium brown but with pale brown longitudinal fasciae. Tibiae of fore legs medium brown along lateral margins, pale sandy colour on anterior margins. Mid and hind tibiae predominantly pale sandy brown. Tarsi pale to medium brown, with claws dark brown.

*Operculae.* Roughly rectangular in form with distal margin obliquely terminated and relatively uncurved; meracantha prominent and relatively acutely terminated; broad ridge extends the length of each opercula from distal to basal area; colour off-white except for small area of brown adjacent to crest around distolateral corners; prominent silver pubescence.

*Timbals.* Four long ribs; rib 4 extends approximately half way across timbal, and is fused dorsally to basal spur; prominent and relatively elongated and ovate grooved dome on timbal plate.

*Abdomen.* General colour pale to darker brown with pale sandy distal margins and inter-segmental membranes. Conspicuous narrow medial concentration of silver pubescence dorsally on all tergites and pygofer, giving appearance of a conspicuous silver dorsal fascia; tergite 2 dominantly medium brown, slightly darker paramedially, with narrow deep brown anterior edge extending to, and partially covering and enclosing the auditory capsules; central area of capsules pale brown; tergites 3 to 8 darker brown in medial and paramedial areas, and sporadically laterally, remaining areas paler

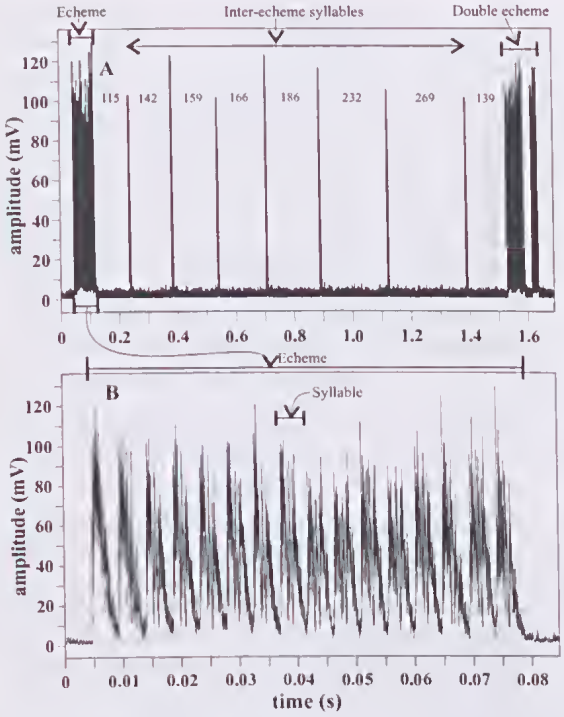


FIG. 31. Time expanded envelope plots of *D. crepitum* songs showing: (a) Two echemes with a series of single inter-echeme syllables. The inter-syllable time intervals are labelled in ms, showing the progressive increase in the intervals. The second echeme represents a double echeme. (b) Expanded time scale envelope plot of the initial echeme in plot (a) showing the sequence of 16 component syllables. Container recording from north side of Pennefather River, filtered (FIR) to 2kHz.

sandy brown with silver pubescence; distal margins and intersegmental membranes of tergites 3-7 conspicuously pale sandy yellow. Sternites pale to medium brown, tending darker in medial areas; sternite II with small black medial area which extends in part to area below auditory capsule; sternite VIII medium brown.

*Pygofer.* Irregularly coloured medium to dark brown. Details as in generic characters.

FEMALE. Fig. 44B. Supra-antennal plate medium brown with short black irregular thin streaks extending laterally from eyes, and a thin black fascia extending inwards from inner eye margins; a medial black fascia extends from between ocelli, through the anterior ocellus and widens adjacent to postclypeus. Remainder of head markings as in male. Pronotum with a central brown fascia which is more diffuse in outline and slightly enlarged at its distal and proximal margins; the markings between and adjacent to oblique fissures are medium brown (not black as in male). Mesonotum with brown paramedial obconical anterior fasciae which coalesce towards anterior margin; the lateral fasciae are relatively indistinct; a pair of small, dark, elliptical paramedial spots lie anterior to each anterior arm of cruciform elevation; the dominant mesonotum colouration is pale-medium brown, with cruciform elevation medium to dark brown along distal and proximal margins, joining anteriorly with a small median fascia. Legs, wings and tergites similar to male, except tergite 2 which lacks any black colouration. Tergite 9 with a pair of paramedial dark brown fasciae extending distally approximately 80-90% of distance towards distal margin. Sternites similar to male, with generally slightly paler colouration. Ovipositor sheath extends approximately 1.5 mm beyond tergite 9.

MEASUREMENTS. N = 14♂, 12♀. *BL*: ♂ 9.1-11.2 (10.4); ♀ 11.2-14.7 (13.4). *FWL*: ♂ 11.2-13.5 (12.6); ♀ 12.2-15.0 (13.8). *HW*: ♂ 3.1-3.7 (3.5); ♀ 3.1-4.0 (3.6). *PW*: ♂ 2.7-3.2 (3.0); ♀ 2.8-3.6 (3.2). *AW*: ♂ 2.9-3.5 (3.2); ♀ 2.5-3.6 (3.1). *FWL/BR*: ♂ 3.07-3.31 (3.20); ♀ 3.18-3.60 (3.39).

DISTRIBUTION & HABITAT (Fig. 13). A very small inconspicuous cicada occurring widely through the Cape York Peninsula, in dense shrub/heath and woodland environments, especially in proximity to water courses. It has also been found in low melaleuca woodland near Normanton. It inhabits the foliage, inner branches and less commonly open trunks of the shrubs and trees, its colouration, its soft and high pitched song, and small size ensuring its very cryptic nature. It is nevertheless locally abundant during the summer (November – March). Specific localities extend from Punsand Bay and the Jardine River in the north; extensively in the Heathlands region (including the Gunshot, Dulhunty, Bertie and Cockatoo rivers and creeks); the Archer River crossing; Pennefather River, north of Weipa; Tozer Gap and the West Claudie River near Iron Range; near Cape Flattery; and to the north of Normanton (southeastern Gulf).

ETYMOLOGY. Latin *crepitum*, a crackle/rattle noise; in reference to the various song forms of this species.

SONG (Figs 30-35). For a very small cicada, this species emits a remarkable range of song patterns

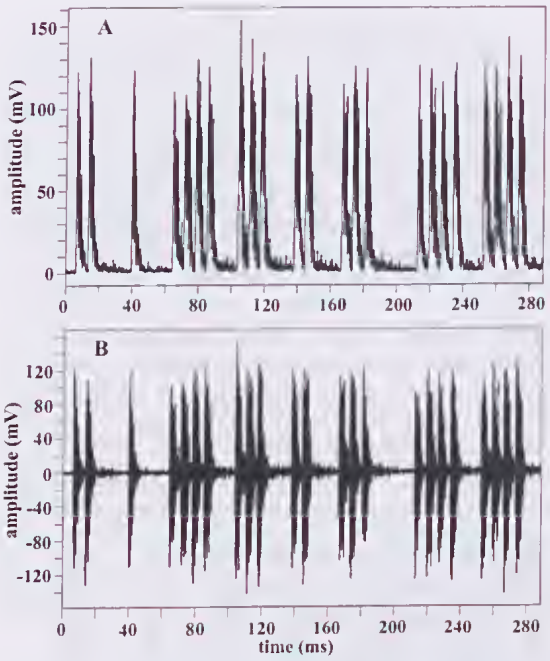


FIG. 32. *D. crepitum*. Envelope curve (a) and waveform plot (b) of the initial stage of syllable coalescence, following the very rapid clicking phase, which leads, with increasing rapidity of song emission, to the continuous buzzing song phase. Recorded from 11km north of Normanton. Container recordings, filtered (FIR) to 1kHz.

(Fig. 30). The simplest pattern, referred to as the *normal clicking song* (Fig. 30A), consists of a series of short, repetitive chirps, referred to as echemes, each ranging between approximately 16 to 86ms in length, comprising between 3 to 16 syllables without clearly defined gaps. The term echeme is used as their lengths and syllable numbers seem to mostly require more than a single cycle of buckling of the timbal pairs. This term, is however, somewhat complicated by the occurrence of the echemes not only singly (most common), but sometimes as sets of double (Figs 30A, 31A) or even triple echemes. For the purposes of the following descriptions, these multiple echeme sets are treated as single echemes unless specified otherwise.

Inter-echeme intervals within the normal clicking song range in length between 0.94-2.26s (Table 6). Within these intervals occur a series of single syllables, 4-11 in number, with inter-syllable intervals of approximately 100-270ms. In detail, these inter-syllable intervals are variable in length, with the most common pattern being one of progressively increasing intervals during song emission, with the exception of the final syllable interval (Fig. 31A).

Under appropriate conditions (e.g. singing in full sunshine; rapidly rising morning temperatures), a significant speeding up of song emission occurs, producing the *rapid clicking song* (sounding to the ear as a distinct 'galloping' song), followed with further increasing rapidity of echeme emission, by the *very rapid clicking song* (Fig. 30B, C). The changes through these song phases involve the reduction in the number of inter-echeme syllables emitted, together with the contraction of the inter-echeme intervals (Table 6). The echemes in these faster song phases mostly occur singly, but in some records, also as double echemes. The song phases further develop, by the progressive coalescence of echemes and syllables (Figs 30D, 32), into the *continuous buzzing song*, with sporadic interspersed very rapid clicking phases. Mean syllable lengths range between 4.6-7.3ms in the normal clicking songs, and 6.1-6.9ms in the faster songs types.

TABLE 6. *Drymopsalta crepitum* - summary of song parameters from three locations. [1] Single and doublet echemes overlap in their respective inter-echeme intervals [2]Figures represent means, ±σ, number of measurements (n) and ranges of data (in brackets).

| | Heathlands | Pennefather River | Normanton |
|---|---|---|---|
| **A. Echemes** | | | |
| ***Inter-echeme intervals -(s)***[1] | | | |
| (i) Normal clicking song | 1.50±0.30 (n=28) (1.01-2.26)[2] | 1.13±0.18 (n=14) (0.94-1.44)[2] | - |
| (ii) Rapid clicking song | - | - | 0.30±0.05 (n=14) (0.20-0.37)[2] |
| (iii) Very rapid clicking song | - | - | 0.25±0.02 (n=16) (0.22-0.28) |

TABLE 6. *(Continued)*

| | Heathlands | Pennefather River | Normanton |
|---|---|---|---|
| ***Inter-syllable intervals (ms) between adjacent echemes*** [1]; [number of inter-echeme syllables in square brackets]. | | | |
| (i) Normal clicking song | 187±22 (n=40) (102-234) [4-11] | 175±42 (n=30) (107-269) [6-8] | - |
| (ii) Rapid clicking song | - | - | 70±21 (n=6) (46-97) [2] |
| (iii) Very rapid clicking song | - | - | 93±9 (n=32) (73-109) [1] |
| **B Echeme structures** | | | |
| ***Individual echeme lengths (ms)***; [number of syllables in square brackets] | | | |
| Single echemes: | | | |
| (i) Normal song | 38.7 [5] to 60.4 [8] | 74.2 [16] to 86.2 [16] | - |
| (ii) Rapid clicking song | - | 112 [19] to 137 [23] | 65.3 [11] to 79.4[13] |
| (iii) Most rapid clicking song | - | - | 57.2 [11] to 64.9[12] |
| Double echemes sets: | | | |
| (i) Normal clicking song | - | 15.8 [3] to 58.8 [14] | - |
| (ii) Rapid clicking song | - | - | 18.6 [3] to 59.0 [10] |
| Triple echemes sets: | | | |
| (i) Normal clicking song | - | 19.4 [4] to 34.0 [7] | - |
| ***Syllable lengths within echemes (ms):*** | | | |
| (i) Normal clicking song | 6.76±0.41 (n=7) (5.9-7.1) | 4.86±0.26 (n=32) (4.4-5.4) | - |
| (ii) Rapid clicking song | - | 5.98±0.09 (n=5) (5.9-6.1) | 5.09±0.10 (n=12) (5.0-5.2) |
| (iii) Very rapid clicking song | - | - | 5.17±0.17 (n=12) (5.0-5.6) |
| (iv) Syllable coalescence (buzzing) phase | - | - | 7.08±0.28 (n=4) (6.7-7.4) |
| ***Syllable structures within echemes:*** | | | |
| Individual hemisyllables – mean lengths (ms) | Not clearly resolvable | 1.4-1.8 (normal song) | (a) 1.07±0.35 (0.66-1.52) (very rapid clicking) |
| **C Inter-echeme single syllable structures:** | | | |
| (i) Mean total lengths - (ms) | 7.26±0.79(n=17) (6.0-9.1) (normal song) | 4.62±0.39(n=16) (4.1-5.8) (normal song) | (a) 6.38± 0.58(n=18) (5.7-7.8) (rapid clicking) |
| | | | (b) 6.12±0.54 (5.7-7.8) (very rapid clicking) |
| | | | (c) 6.85±0.27(n=22) (6.16-7.38) (coalescence phase) |
| (ii) Hemisyllable mean lengths -(ms) | 3.28±0.40(n=17) (2.8-3.4) (normal song) | 2.13±0.11(n=16) (2.0-2.4) (normal song) | (a) 0.47±0.19(n=48) (0.17-0.90) (rapid clicking) |
| | | | (b) 0.44±0.11(n=43) (0.27-0.71) (very rapid clicking) |
| | | | (c) 0.85±0.43(n=52) (0.28-1.71) (coalescence phase) |

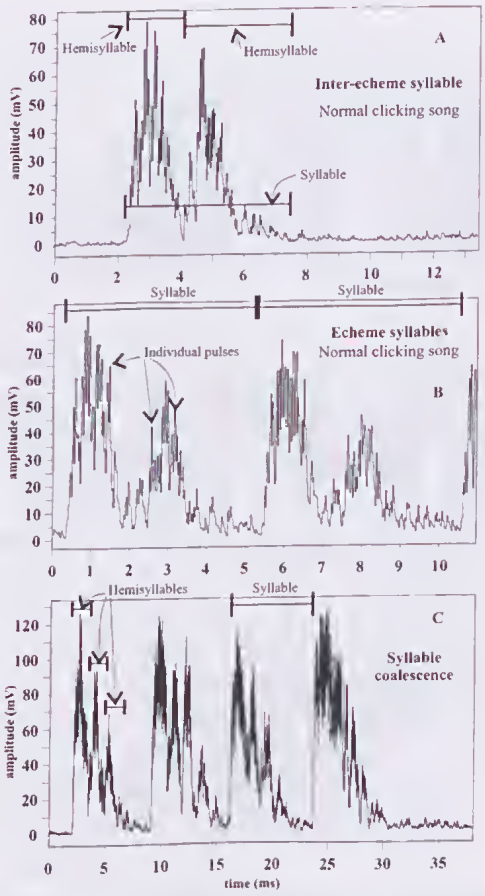


FIG. 33. *D. crepitum*. Expanded time scale envelope curves showing; (a) details of an inter-echeme syllable structure of the normal clicking song showing two hemisyllables; (b) two syllables within an echeme of the normal clicking song, each with two hemisyllables; and (c) four syllables from the pulse coalescence phase leading to the continuous buzzing song (see Fig. 32), each syllable showing three or more hemisyllables. Within the hemisyllables shown within the three plots, the complex higher frequency carrier pulses are visible; selected pulses labelled in (b) and selected hemisyllables labelled in (c). (a) and (b) represent container recordings from the northern shore of Pennefather River; (c) is a container recording from 11km north of Normanton. Each record is filtered (FIR) to 1kHz.

In time expanded plots, the majority (but not all) of the inter-echeme syllables of the normal clicking song display two well defined component hemisyllables (Fig. 33A), with lengths between 2-4ms (250-500Hz). In the rapid clicking ('galloping') song, the inter-echeme syllables vary between one to two in number (most common), and rarely three (Fig. 30B). Single inter-echeme syllables characterise the very rapid clicking songs (Fig. 30C). In the coalescence phase leading to buzzing, the progressive coalescence of the syllables (Figs 32, 33D) becomes evident. Within these more rapidly emitted song phases, the internal syllable structures move away from the double hemisyllables of the normal clicking song to more complex multiple hemisyllable structures (Figs 33C, 34) whose lengths range between 0.17-1.7ms (0.59-5.9kHz). The hemisyllables themselves comprise finer scale (higher frequency) pulses, representing the various carrier wave pulses (Figs 33, 34) whose wavelengths lie between approximately 0.06-0.25ms (~4-16.7kHz). The important aspect is that with increasing song emission rates, there is a recognisable change in pulse structures, consistent with the amplitude spectral data discussed below.

The echemes represent the coalescence of syllables (Fig. 31B), each normally with two hemisyllables in the normal clicking song (Fig. 33B), similar in structure to the inter-echeme syllables. In the rapid and very rapid clicking songs, however, the double hemisyllable structures tend to change towards multiple, shorter hemisyllables as seen in the associated inter-echeme syllables (see above). Syllable lengths vary between 4.4-7.4ms (Table 6), there being overlap of the data between the normal clicking and the faster song types, and also with the inter-echeme syllable lengths. The syllable structures comprising the echemes and inter-echeme syllables are clearly very similar.

Amplitude spectra (Fig. 35A) are especially complex in the normal clicking song, with two dominant peak groupings between ~12-13.5 and ~14-16 kHz. Further broad multiple peaks occur at ~16.5-17.5, 11-11.5, 8-8.5, and 7.5 kHz. Some of the observed complexity may represent multiple side band peaks originating from the complex hemisyllable through to echeme structures and amplitude modulation rates. Nevertheless, the range of frequencies presumably represents sound radiation from multiple sound radiation structures (Fonseca & Popov, 1994; Fonseca & Bennet-Clark, 1998). Comparison of the spectra of the normal song with those of the continuous buzzing phase (syllable coalescence phase; Fig. 35C) shows a marked amplitude increase of a broad peak centred at 15.2 kHz, but a notable amplitude reduction of all the other peaks. Nevertheless,

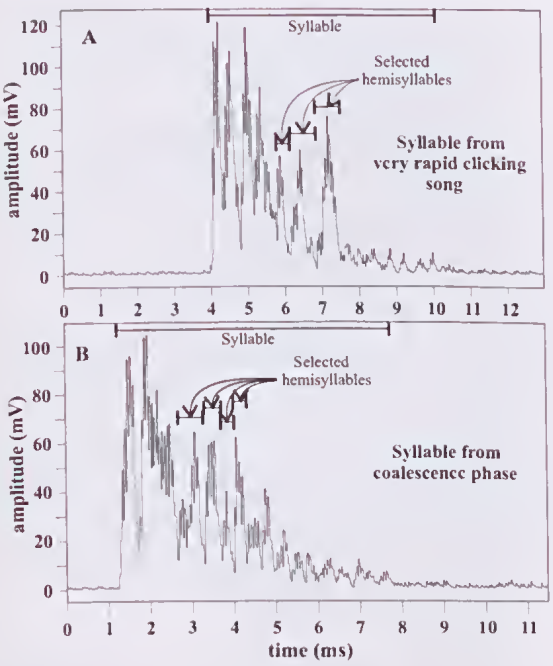


FIG. 34. *D. crepitum*. Expanded time scale envelope curves showing detailed structures of: (a) an inter-eceheme syllable from the very rapid chirping song phase, and (b) single syllable from the syllable coalescence phase leading to the continuous buzzing song. In both plots, the syllables are characterised by multiple hemisyllables of variable lengths (cf. Figs 33A, B). Selected hemisyllables labelled. Container recordings from 11km. north of Normanton, filtered (FIR) to 1kHz.

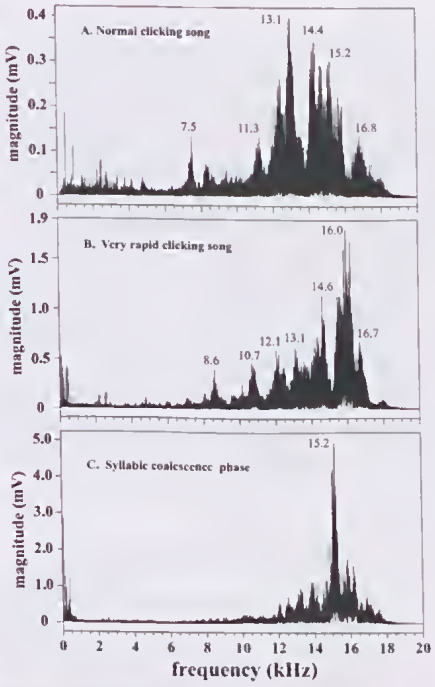


FIG. 35. Amplitude spectra of *D. crepitum* songs, showing the shifting emission frequency patterns in the changing song phases; (a) normal clicking song, filtered (FIR) to 0.5kHz; (b) very rapid clicking song, unfiltered; (c) syllable coalescence phase leading to buzzing song, unfiltered. Container recordings from (a) northern shore of Pennefather River, and (b, e), 11km north of Normanton. The frequencies of the main peaks are labelled (kHz).

weak peaks centred at 12, 12.5, 13.2, 13.9, 14.7, 15.9 and 16.9 are evident.

The major peak at 15.2 kHz is inferred to represent the fundamental frequency. Although a complex of peaks coincides with this frequency in the normal clicking song, the maximum frequency amplitude of the latter lies at ~13 kHz. It therefore seems possible that with increasing speed of song production, there is a change in the relative importance of the various sound radiating structures, with or without a change in the fundamental frequency. Amplitude spectra of the rapid chirping and most rapid chirping phases exhibit intermediate stages in the relative reduction of the frequency peaks less than ~15 kHz, as shown in Fig. 35B by the very rapid chirping phase. This clearly exhibits the reduction of the 13 and 14-14.8 kHz peaks, and the enhancement of the 15-16 kHz peaks (the latter inferred to represent the carrier frequency). Thus, the amplitude spectra, when considered through the sequence of increasing syllable emission rates, suggest a general increase in the carrier frequencies and corresponding reduction of the lower frequency components, consistent with changing patterns of sound radiating centres, and apparently correlated to the greater importance of timbal radiation.

It is noted that the timbal rib structure of this species is relatively simple with four long ribs and three poorly developed short ribs (Fig. 29C). Ribs 1-3 are fused ventrally and dorsally, whereas rib 4 is fused only dorsally to the basal spur. It is therefore suggested that the fused posterior long ribs act, in unison, as the dominant sound producing mechanism.

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FIG. 36. *Crotopsalta plexis*. A, male, from near Chinchilla, 10.5mm long; B, female, Glebe Weir near Taroom, 11.8mm long.

FIG. 37. *Crotopsalta fronsecetes*. A, male, from Gurulmundi, north of Miles, 11.7mm long; B, female from 9 km northwest of Yaamba, 12.0mm long.

FIG. 38. *Crotopsalta strenulum*. A, male; B, female, from Nogoa River, Emerald, central Queensland. Total body lengths 10.3 and 11.2mm, respectively.

FIG. 39. *Crotopsalta poaecetes*. A, male; B, female, from Cloncurry, northwestern Queensland. Total body lengths 10.0 and 10.9mm, respectively.

FIG. 40. *Gagatopsalta auranti*. A, male; B, female. From northern Barakula State Forest, north of Chinchilla, southeast Queensland. Total body lengths 10.6 and 11.1mm, respectively.

FIG. 41. *Gagatopsalta obscurus*. A, male; B, female. From Milroy H.S., approximately 70km north of Quilpie, southwest Queensland. Total body lengths 12.3 and 13.4mm, respectively.

FIG. 42. *Caliginopsalta percola*. A, male, from northern Barakula State Forest, north of Chinchilla, 11.6mm long; B, female, from Lake Broadwater, near Dalby, 12.3mm, long.

FIG. 43. *Pipilopsalta ceuthoviridis*. A, male, from Cluny lagoon, near Bedourie, 12.6mm long; B, female, from the Thompson River, near Jundah, 12.9mm long.

FIG. 44. *Drymopsalta crepitum*. A, male, from Heathlands H.S., 10.6mm long; B, female, from the northern side of Pennefather River, northern Cape York Peninsular, 12.2mm long.

# *CARYBDEA ALATA* AUCT. AND *MANOKIA STIASNYI*, RECLASSIFICATION TO A NEW FAMILY WITH DESCRIPTION OF A NEW GENUS AND TWO NEW SPECIES

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The species recognition criteria have been confused for eubomedusae, leading to underestimates of biodiversity and nomenclatural errors in the group. At least nine different species have been described with crescentic gastric phaecllae, T-shaped rhopaliar niche ostia, and/or 3 velarial canals per octant; all were subsequently included in the synonymy of the oldest name, *Carybdea alata*, which lacks both a type specimen and an unambiguous identity. To stabilize the nomenclature of the group, the new genus *Alatina* is proposed based on a common form for which type material and DNA sequences are available. Two species from northern Australia are herein described for the genus. The other nine species previously associated with the name *Carybdea alata* are herein reevaluated and determinations are made as to their validity. The validity of another species, *Manokia stiasnyi*, has been questioned, and was not previously appreciated as belonging to this morphogroup. Reexamination of the holotype confirms that the taxon is distinct, and allied to *Alatina*; a redescription is provided. A new family, Alatinidae, is proposed to accommodate *Alatina* and *Manokia*. The family Carybdeidae and the genus *Carybdea* are redefined. □ *Taxonomy, Irukandji syndrome, Cubozoa, box jellyfish, Australia.*

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*Carybdea alata* Reynaud, 1830, has been the most problematical of all cubozoan species, from nomenclatural and practical perspectives. The species was erected for a medusa collected somewhere in the South Atlantic, on the basis of a watercolour by Reynaud in Lesson (1830). It was widely disregarded as unrecognizable, until the name was revived by Vanhöffen (1908) in the interest of stability. Unfortunately, Vanhöffen failed to assign a particular specimen or suite of characters to the name, and the species originally assigned that name is unrecognizable. By the time of Kramp's Synopsis (1961), the nominal species *C. alata* was recognized by its crescentic phacellae and three well developed scales enclosing the rhopalial niches. Other authors additionally recognized three velarial canals per octant as diagnostic (Mayer, 1910; Bigelow, 1938). The problem is that many different forms share these characters, even though they barely resemble one another overall. This makes identification very easy for the lay person, but it does not reflect biological reality and makes for confusion that has yet to be resolved.

At least nine different nominal species have been described with crescentic phacellae and/or three canals per octant and/or three well developed covering scales. Haeckel (1880) recognized six species with these characters, including five new ones (*Procharybdis tetraptera*, *Procharybdis turricula*, *Carybdea pyramis*, *Carybdea philippina*, and *Carybdea obeliscus*). Agassiz & Mayer (1902) added *C. grandis*, based on its very large size. Mayer (1906) added *C. moseri*, based on short basal stalks of the pedalia and differently shaped pedalial wings, though Bigelow (1909) regarded it as a young stage of *C. grandis* and Mayer (1910) concurred. Menon (1930) added *C. madraspatana*, based on its apical concavity and greater number of velarial canals. Kramp (1961) lumped them all under the oldest available name, *C. alata*. Historical confusion and instability concerning *alata*-group relationships have apparently been based on failure to recognize the crescentic phacellae as common to more than one species, and reluctance to regard geographically variable characters as informative.

*Manokia stiasnyi* (Bigelow, 1938), also possesses crescentic phacellae and three well developed covering scales, though the former character was not previously appreciated. The species was defined on the basis of its branched tentacles and its similarity to *Carybdea alata* was

not noted. Different authors have held different opinions about the validity of this species without examining the type specimen (Southcott, 1967; Kramp, 1968). I have examined the holotype, and believe the species is worthy of recognition.

It is difficult to say how many different species under the name *Carybdea alata* can be distinguished worldwide, because typically every specimen with crescentic phacellae has been lumped into the one nominal species, with typically very little discussion about other characters. However, at least three different species exist in the southwestern Pacific off Australia and New Guinea, and that these differ from several earlier described forms. To stabilize the nomenclature of *Carybdea alata* auct., I propose reclassification of species with crescentic phacellae and T-shaped rhopaliar niche ostia, defined on the basis of a well characterized type species for which type specimens and DNA sequences are available. Thus, I propose *Alatina* nov. with *A. mordens* sp. nov. and *A. rainensis* sp. nov. The other nine species previously associated as *Carybdea alata* are re-evaluated and determinations are made as to their validity. Problematical *Manokia stiasnyi* (Bigelow, 1938) is redescribed based on the type specimen. Together, *Alatina* and *Manokia* appear to form a natural group separate from *Carybdea* and other carybdeids. For this group I propose Alatinidae fam. nov.; the separation of the groups is supported by 18S rDNA analysis (personal observations). Revised definitions of the Carybdeidae and *Carybdea* are given.

## MATERIALS AND METHODS

All taxonomic observations and measurements were made on preserved material, unless otherwise noted. Measurements were made with Max-Cal digital calipers to the nearest 0.01mm; in some cases, an available absolute measurement was clearly not the correct full measurement (e.g., in the case of a brittle, folded specimen), denoted with + following the measurement. Bell height (BH) was measured from the apex of the bell to the velarial turnover. Diagonal bell width (DBW) was measured across diagonally opposite pedalia on a flattened specimen, at the height of the pedalial lamella. Interrhopalial width (IRW) was measured between adjacent rhopalia, with the specimen flattened. Tentacle base width (TBW) was measured across the widest diameter at the uppermost part of the tentacle, immediately below the pedalium. Pedalial dimensions are as follows: length (PL) from the subumbrellar lamella to the tentacle insertion, width (PW) and canal width (CW) at the vertical midpoint. Sex was determined, when possible, by biopsy. Female gonads have obvious ova; male gonads have a conspicuous "finger-print" appearance of many fine more-or-less parallel lines. Phacellae were examined by making a small incision in the upper corners of the bell, and then pulling back a small amount of mesoglea to expose the phacellae in situ, or by opening up the full length of the body wall to expose the stomach. Nematocysts were examined and measured with a Leica DMLB compound microscope and Leica IM-50 Image Manager v. 1.20 for Windows; all observations and photographs were made through a 40x objective, unless otherwise specified. Nematocysts were identified following the keys of Calder (1974), Mariscal (1971) and Williamson et al. (1996). Translations of the original German descriptions of *M. stiasnyi* and Haeckel's species were made with Globalink Power Translator 6.0 for Windows.

Throughout the text, "*alata*" has very restricted meaning. *Carybdea alata* refers to the species named by Reynaud, or to specific contextual meanings of other authors, but *Carybdea alata* auct. refers collectively to the species grouped under this name by various other authors. The term "*alata*-group" refers to the loosely defined collection of described and undescribed forms that have been identified as *Carybdea alata* by traditional criteria (including museum collections and published identifications), but are not yet clearly internal or external to *Alatina*.

ABBREVIATIONS: Australian Institute of Marine Science (AIMS); Great Barrier Reef (GBR); Institut Royal des Sciences Naturelles de Belgique, Brussels (IRSNB); James Cook University (JCU); Museum of Comparative Zoology, Harvard (MCZ); Museum of Tropical Queensland, Townsville (MTQ); Queensland Museum, Brisbane (QM); South Australian Museum, Adelaide (SAM); and United States National Museum, Washington DC (USNM). In synonymies I follow Matthews (1973); "v" indicates that I have seen the material referenced and "v*" indicates that I have seen the type.

TABLE 1 (facing). Comparison of main diagnostic characters in the Carybdeida.

| Species | Phacellae | Rhopalial niche ostium | Pedalial canal | Velarial canals (per octant) | Principal tentacular nematocysts | Other distinguishing features |
|---|---|---|---|---|---|---|
| *Alatina* spp. | Crescentic, with long cirri | T-shaped | Simple, rounded or angular | 3, typically simple, or only slightly branched distally | Eurytcles, isorhizas | Tall, narrow, flimsy body; very wide pedalial wings; lacking perradial mesenteries |
| *Carukia barnesi* | Lacking | Frown-shaped | Simple | 2, simple | Lemon-shaped tumitcles | Neckerchief-like tentacle bands; with rhopalial "horns"; narrow pedalia |
| *Carybdea rastonii* | Multiple-stalked oblique row | Heart-shaped | Knee | 2, dendritic | Football-shaped eurytcles and small ovoid isorhizas | Single row of nematocyst freckles on outer pedalial wing; pedalia scalpel-shaped |
| *Carybdea marsupialis* | Multiple-stalked epaulette | Heart-shaped | Knee | 3-4, dendritic | Unknown | Single row of nematocyst freckles on outer pedalial wing; pedalia scalpel-shaped |
| *Carybdea sivickisi* | Crescentic, cirri singly rooted | Vertical oval | Simple | 2, paw-like | Football-shaped eurytcles, large and small ovoid isorhizas | Adhesive pads on top of exumbrellar; single row of nematocyst bars on outer pedalial keel; narrow pedalia |
| *Carybdea xaymacana* | Single-stalked epaulette | Heart-shaped | Knee | 2, of two types | Large club-shaped eurytcles, small ovoid isorhizas | Single row of nematocyst freckles on outer pedalial wing; pedalia scalpel-shaped |
| "Darwin carybdeid" | Lacking | Frown-shaped | Thorn | 4, paw-like with long, parallel fingers | Club-shaped type 4 microbasic p-mastigophores | With rhopalial "horns"; with well developed perradial mesenteries; pedalia broadly rounded |
| *Manokia stiasnyi* | Crescentic | T-shaped | Small nub at bend | 4, simple and undulating | Subspherical eurytcles | Tentacle bands with lateral extensions; with scalpel-shaped pedalia |
| "Morbakka" | Lacking | Frown-shaped | Thorn | Feather-like, too many to count | Club-shaped type 4 microbasic p-mastigophores; football shaped isorhizas | 2 eyes per rhopalium; with perradial lappets and rhopalial "horns"; with well developed perradial mesenteries; pedalia relatively narrow |
| *Tamoya haplonema* | Vertical | Frown-shaped | Thorn | Numerous | Unknown | 6 eyes per rhopalium; lacking perradial lappets and rhopalial "horns"; with well developed perradial mesenteries; pedalia long and well rounded on both sides |
| *Tripedalia* | Single-stalked epaulette | Shallow frown-shaped | Simple | 3-4, simple | Eurytcles, stenotcles and spherical & non-spherical isorhizas | Two or three pedalia per corner; with weak perradial mesenterics; pedalia narrow |

## SYSTEMATICS

Phylum CNIDARIA Verrill, 1865
Subphylum MEDUSOZOA Petersen, 1979
Class CUBOZOA Werner, 1973
Order CARYBDEIDA Maas, 1909 sensu Werner, 1984
Family ALATINIDAE nov.

TYPE GENUS. *Alatina* gen. nov.

DIAGNOSIS. Gastric phacellae crescentic, comprised of long cirri arranged more or less parallel in a single plane; with T-shaped rhopalial niche ostia, comprised of a single upper covering scale and 2 lower, well developed covering scales; with 3 or 4 more or less simple velarial canals per octant; with a shallow stomach, completely lacking perradial mesenteries.

### **Alatina** gen. nov.

TYPE SPECIES. *Alatina mordens* sp. nov.

ETYMOLOGY. From the specific name of *Carybdea alata* Reynaud, 1830, with the suffix *-ina* (diminutive, Latin). Feminine.

DIAGNOSIS. 3 velarial canals per octant; tentacles simple.

REMARKS. *Alatina* spp. are easily distinguished from other carybdeids by several conspicuous features, especially the crescentic phacellae and their long cirri, the hemispherical adaxial pedalial wings, the T-shaped rhopaliar niche ostia, the three simple or end-branched velarial canals per octant, and the flimsy gelatinous consistency of the body. In contrast, *Carybdea* spp. have epaulette-shaped or linear phacellae of short cirri, scalpel-shaped pedalia, heart-shaped rhopalial niche ostia, 2-4 branched velarial canals per octant, and a relatively springy bell consistency that holds its shape in water. *Tripedalia* spp. have multiple simple pedalia. *Tamoya* is characterized by having vertical phacellae in the interradial corners of the stomach wall. *Carukia* and several other undescribed forms are characterized by lacking phacellae altogether. *Tripedalia*, *Tamoya* and *Carukia* all have frown-shaped rhopaliar niche ostia (Table 1). Species of *Carybdea* are detailed because there is historically great confusion on how to tell them apart. A revision of *Carybdea* with additional species is to be published elsewhere, and is beyond the scope of this paper.

Regrettably, it is impossible to say with certainty which of the Atlantic forms is the true *C. alata* of Reynaud, but it is clear that not all forms of *C. alata* auct. should be considered the same species. One must start sorting out the confusion somewhere, and because I have multiple local specimens at my disposal, along with their DNA, it seems most prudent to begin with these. It is my hope that by establishing a workable system in which to incorporate other species, it will eventually be possible to differentiate the large number of regionally distinct forms.

*Alatina moseri* (Mayer, 1906) from Hawaii is redescribed based on type and non-type material. The other eight species of *Alatina* are treated briefly and compared (Table 2). Although some remain unidentifiable, most forms previously described and associated with *C. alata* auct. should be considered valid until proper comparison of material from the different type localities can be made.

### **Alatina mordens** sp. nov.
(Figs 1, 2)

Unidentified species, v?Mulcahy, 1999: 88 [Irukandji syndrome case requiring life support]; v?Little et al., 2001: 178 [case history of sting, life support required for 8 days]; ?Taylor et al., 2002: 175 [Irukandji syndrome with persistent symptoms over 7 months].

MATERIAL EXAMINED. HOLOTYPE: QMG55282, Moore Reef, GBR, QLD (approx. 16°52.160'S 146°12.353'E), coll. 13 November 1998; immature male, BH 80.79, DBW 64.42, IRW 30.07, TBW 2.45; forwarded by J. Seymour; captured within minutes of severe Irukandji sting reported by Mulcahy, 1999 (Fig. 1A).

PARATYPES: SAMH1013, same data as holotype; BH 74.09, DBW 54.22, IRW 25.29, TBW 1.89 (Fig. 1B). SAM H1053, Osprey Reef, Coral Sea, QLD (approx. 13°54.190'S 146°38.985'E), 29 January 2000; BH uninterpretable due to damage, DBW 47.75, IRW 24.06, TBW 1.94; forwarded by P. Colwell; captured within minutes of Irukandji stings; examined live and preserved. QMG317058, Agincourt Reef, GBR (approx. 16°01.907'S 145°51.203'E), coll. 24 April 1998, forwarded by R. Hore; BH 80.44, DBW 64.05, IRW 30.93, TBW 2.13. QM G317059, same data as QMG317058; BH 59.22, DBW 41.24, IRW 22.40, TBW 1.05. AIMS 2003-10, Agincourt Reef, GBR, 28 April 2003; BH ca. 75, DBW ca. 55; forwarded by R. Hore, captured following superficial sting of 12 year old boy. QM G55288, Agincourt Reef, GBR, 25 August 2003; immature male, 85mm BH, 65mm DBW, 32mm IRW; forwarded by R. Hore.

TABLE 2 (facing). Comparison of *Alatina* species. Data based on original descriptions and figures.

| | Maximum BH | Bell nematocysts | Velarial canal # per octant | Velarial canal form | Pedalial canal bend | Pedalial nematocysts | # of eyes | Other characters |
|---|---|---|---|---|---|---|---|---|
| *A. alata* comb. nov. | ? | ? | ? | ? | ? | ? | ? | |
| *A. grandis* comb. nov. | 230mm | Apparently absent | 3 | Short, branched tree-like | 90° | Apparently absent | 1 in adults; 3 in juvs | |
| *A. madraspatana* comb. nov. | 110mm | Small | 5 | Branched | Simple | Sometimes; small | 6 (1 lensed) | Apical concavity |
| *A. mordens* n. sp. | 96mm | Small | 3 | Simple, biforked, triforked at tip | Rounded | Minute | 2 median | Pedalial wings wide |
| *A. moseri* comb. nov. | 80mm | Present | 3 | Simple/biforked | Simple | Absent or 1 row oblong | 4 | Paired cirri in phacellac |
| *A. obeliscus* comb. nov. | 35mm | ? | 3 | Simple beside frenula, forked beside pedalia | ? | ? | ? | Tentacles thickened at end |
| *A. philippina* comb. nov. | 30mm mature | Apparently absent | 3 | Simple, short | Simple to angular | Apparently absent | ? | Split phacellac; long pedalia |
| *A. pyramis* comb. nov. | 30mm mature | Apparently absent | 3 | Simple, wide | Apparently simple | Apparently absent | 6? | Pedalial wings narrow; frizzy lips |
| *A. rainensis* n. sp. | 18mm mature | Minute | 3 | Simple | 90° | Absent | 4 | Butterfly-form gonads |
| *A. tetraptera* comb. nov. | 30mm mature | Apparently absent | Lacking | Lacking | Simple | Apparently absent | 1 | Split wing-like phacellac; very long, large pedalia |
| *A. turricula* comb. nov. | 170mm | Apparently absent | Apparently absent | — | Simple to angular | Apparently absent | ? | Overhanging pedalial wings |

OTHER MATERIAL EXAMINED. [JCU1] Unregistered specimen at JCU Cairns, QLD, same data as holotype; BH 61.32, DBW 53.53, IRW 22.83, TBW 1.77 (Fig. 1C). [JCU 2] Unregistered specimen at JCU Cairns, QLD, coll. Agincourt Reef, GBR, 6 July 1991; BH 96.06, DBW 69.72, IRW 31.77, TBW 1.75. Approximately 20 specimens frozen or in ethanol, caught at various times at Agincourt Reef, GBR, 2000-2004, examined casually before being forwarded for venom analysis.

TYPE LOCALITY. Moore Reef, outer Great Barrier Reef.

ETYMOLOGY. Latin *mordax*, biting; in reference to the painful sting.

DIAGNOSIS. Bell tall, tapered, apically truncate, with exumbrellar nematocyst freckles; with crescentic phacellae, comprising many tufts of long cirri which branch only near the root; with 3 straight, simple to triforked velarial canals in each octant, bearing a row of 1-5, typically 1-3, small, round nematocyst freckles on root area; with broadly rounded adaxial pedalia keels; with simple rounded pedalial canal.

DESCRIPTION OF HOLOTYPE. Bell much taller than wide, with overall shape of a truncate tall pyramid, of thin and flimsy gelatinous consistency (Fig. 1A-C). Apex much narrower than velarial aperture; flat to slightly rounded. Exumbrella with sparsely scattered minute, unraised, round nematocyst freckles; with interradial furrows shallow and wide, extending along entire bell height. Adradial furrows lacking. Phacellae (Fig. 2A) 4, interradial, crescentic, broad, with numerous long gastric filaments arranged in a more or less parallel fashion in a single plane. Rhopalial niches (Fig. 2B) 4, perradial, flush with exumbrellar bell wall, shallowly convex on subumbrellar wall; with T-shaped ostia, i.e., 1 covering scale above and 2 well-developed scales below. Upper covering scale thickened, protruding slightly from bell wall, broadly convex in contour; lower scales well developed, with vertical opposing edges, separated by a furrow continuing to velarium; upper and lower scales separated horizontally by a discontinuity on each side of ostium. Rhopalial horns lacking. Rhopalial stem without warts. Rhopalial lens and eyespot morphology indeterminable in holotype without dissection; due to very large size of lower eye, rhopalium appearing as a single black spot to unaided eye. Pedalia (Fig. 2C) 4, interradial, with short stalk; with large round adaxial keel approximately 3-4x pedalial canal width, overhanging at point of tentacle insertion; with narrow abaxial keel approximately 2x canal width; with few scattered minute nematocyst freckles. Pedalial canals bowed slightly toward abaxial keel, narrow, laterally flattened; with rounded to slightly angular bend near point of origination from bell, straight or slightly tapered into tentacle. Velarium wide, with nematocysts confined to single row of small, round warts on adperradial velarial canals only. Velarial canals (Fig. 2D) 3 per octant, simple throughout most of length, may be biforked or triforked at distal end; 4-6 extensions reaching margin or nearly so in each octant; canal roots (velarial extensions of gastric pouches) 3 per octant, narrow, extending onto velarium approximately halfway to margin. Perradial lappets lacking. Frenulum a single, narrow, stiff sheet, extending only about halfway onto velarium, with a narrow strip of thickened tissue extending almost to velarial margin. Gonads attached along entire length of interradial septa; leaf-like, extending laterally into radial stomach pouches; narrow in this immature male specimen. Tentacles (Fig. 2E) 4, 1 per pedalium, hollow, round in cross section, with nematocysts in alternating bands (larger, smaller, larger, etc.); preserved, tentacle constricted approximately every 10 bands, giving segmented appearance, though unclear whether this is an artifact of contraction and preservation; length in life unknown. Stomach small, flat, extending into 4 large coelenteric pouches, divided by interradial septa. Interradial septa without minute perforations. Manubrium short. Color: preserved in formalin, the gonads, tentacles, rhopalia, and phacellae opaque whitish; body slightly cloudy.

The exact nature of several characters could not be ascertained in the holotype without dissection, which was considered inadvisable, e.g., the phacellae (number of roots, branching pattern of cirri bundles), the eyes (number and arrangement), the manubrium (cross section shape, length and shape of lips), and mesenteries (length and state of development). With strong side light, I was able to determine with reasonable confidence that the mesenteries do not extend down along the middle regions of the bell wall; however, it is not unusual for taxa to have weakly developed mesenteries in the perradii of the manubrium which only extend a short distance. Whether this is the case in *A. mordens* cannot be determined from the holotype. It is unfortunate that the number of roots to the phacellae could not be examined; this will likely be an important species discriminator. In paratype QMG55288, these missing characters were scored as follows: phacellae with

about 20 roots per group; cirri long, bundled near the base in clusters of several; eyes 4 per rhopalium, two lensed median plus one slit-eye on each side; manubrium open and amorphous; lips wide triangular; mesenteries completely absent in flap or cord form. Some specimens of this species have only two median eyes and no lateral eye spots, while one specimen has the normal cubozoan 6 eyes (2 median lensed eyes, 4 lateral eye spots); it would appear that the lateral eye spots are somewhat variable, but the lower main eye is always unusually large in comparison to other Carybdeida. The gonads of sexually ripe specimens are overlapping and pleated (Fig. 1B). In life, the body is completely transparent and colorless, and the tentacles are bright pink.

STATOLITH (Fig. 2F, paratype #AIMS 2003.10). Tear-drop-shaped, with a medially incised, truncate basal border, deep garnet reddish in colour; enclosed in lower portion of rhopalium, situated immediately behind the main lens rather than below it. The statolith is orientated truncate-side down for standardized comparison with statoliths of other species; however, *in situ* the truncate side is orientated up toward the rhopalial stalk and the flat side facing the camera in the photograph is the unexposed side, facing the back of the main eye *in situ*.

CNIDOME (Fig. 7A, B; from paratype QMG55288). The tentacular nematocysts are exclusively lemon-shaped eurytele, with an arithmetic mean of 22.96$\mu$m long by 12.77$\mu$m wide (range 19.30-27.25$\mu$m long x 11.10-14.85$\mu$m wide, N=57). The bell nematocysts are exclusively large spherical isorhizas with a short, loosely coiled tubule, averaging about 12 per nematocyst freckle; the arithmetic mean size is 30.34$\mu$m (range 28.25-31.71$\mu$m, N=24). Nematocysts of the lips and gastric cirri were not observed, despite efforts to find them.

NUCLEOTIDE SEQUENCES. Most of the 18S rDNA gene has been sequenced for 4 specimens (L. Peplow, unpubl. data).

DISTRIBUTION. Anecdotal reports from throughout the northern outer Great Barrier Reef (GBR) region; confirmed from Moore and Agincourt Reefs, on the outer GBR, and from Osprey Reef in the Coral Sea.

REMARKS. This species is distinguished from other carybdeid genera in nearly every scorable character (Table 1). Only rudimentary comparison can be made with other species that have previously been associated with *C. alata* auct., due to insufficient descriptions and lack of comparative material (Table 2).

The relationships of *Alatina* spp. will not be fully understood until fresh collections are made from type localities and rigorous morphological and molecular comparative studies are made. Particular attention should be given to the number of roots to the gastric phacellae, the branching pattern or lack thereof to the velarial canals, the number of lensed eyes and eye spots at maturity, and patterns of exumbrellar, pedalial, and velarial nematocyst clusters.

LIFE CYCLE. Unknown. However, Arneson & Cutress (1976) described the life cycle of *C. alata* from Puerto Rico. Similarities may emerge when the life history of *A. mordens* is resolved, presumably being closely related.

ECOLOGY. Unknown. However, another species of uncertain identity in the *Alatina* clade, studied in Hawaii, occurs in large numbers 9-10 day after the full moon (Thomas et al., 2001). Preliminary study indicates that *A. mordens* has a similar predictability (R. Hore, pers. comm. June 2004).

SEASONALITY. Collection records indicate that *A. mordens* can be encountered any time of the year on the outer Great Barrier Reef, contrary to local folklore which holds that one is only at risk of stings during the summer months, and then only onshore. Furthermore, collection records do not appear to correlate season with size or maturity, indicating that perhaps *A. mordens* breeds and grows all year.

MEDICAL NOTES. *Alatina mordens* may pose a serious human health risk; however, correlations are ambiguous and experimental evidence supporting or refuting this hypothesis is lacking. There are several known cases of severe Irukandji symptoms following envenomation on the outer reef, with similar case histories and *A. mordens* being captured or sighted at the time. Typically, this species is encountered at night, when it swarms near lights used for scuba diving; some stings occur when scuba divers return to the boat and swim up into a swarm of jellyfishes. Severe envenomations in cases involving diving may be mistaken for decompression sickness (Williamson, 1985; Hadok, 1997). The outer reef symptoms typically onset quickly (ca. 5-10 minutes), and resemble a more severe version of the Irukandji Syndrome than is typically

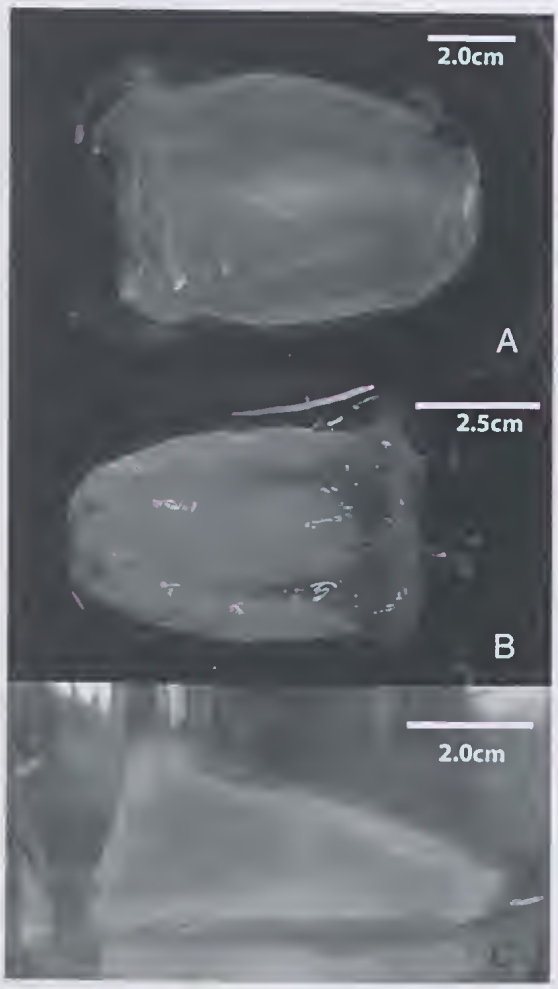


FIG. 1. *Alatina mordens* gen. et sp. nov., different forms of general appearance. A, Holotype QMG55282, laying flat, with immature gonads. B, Paratype SAM H1013, laying flat, with ripe, pleated gonads. C, Unregistered JCU specimen from Moore Reef, GBR, normal pyramidal appearance, as in life.

associated with coastal envenomation, often involving severe hypertension (unpubl. data).

In at least one outer reef case, the victim saw herself get stung by a large jellyfish in the water (Anonymous, pers. comm., Dec. 1998); three specimens retrieved at the time of the incident comprise the holotype, a paratype (SAMH986), and the first of the two JCU non-type specimens listed above. The patient was critically ill for more than a week following envenomation (Mulcahy, 1999; Little et al., 2001). A single nematocyst recovered from the victim's skin was later (Little & Seymour, 2003) attributed to an unnamed species in the Queensland Museum collection previously identified by me. The nematocyst from this sting event (Little & Seymour, 2003) cannot be differentiated from those characteristic of *A. mordens* (Fig. 7); thus, the possibility that this species was responsible for the sting must be considered.

In another case from which the same species was recovered, 5 divers were stung at Osprey Reef the night of 29 January 2000, while surfacing into the swarm at the end of the dive; the onset of symptoms was rapid (ca. 5 minutes) and all required medical treatment (P. Colwell, pers. comm., Feb. 2000). A single specimen was captured from those that were swarming at the time, and was forwarded to me for study (SAM H1053). A third case of similar circumstances at Hastings Reef on New Years Eve 1999, involving 2 victims, was also reported (P. Colwell, pers. comm., Feb. 2000); no specimens were retained. Other anecdotal cases exist in which similar jellyfish were sighted but not captured, and which involved severe Irukandji syndrome (unpubl. data). While the evidence from multiple sting events lends support to this species being the stinging agent, it is important to note that this species is only possibly the cause of these cases of Irukandji syndrome; testing this hypothesis experimentally should be considered a high priority for stinger management.

There is also some indication that *A. mordens* is not especially dangerous. Paratype #AIMS 2003.10 was captured following a superficial sting to a 12 year old boy, in which no systemic symptoms were reported (R. Hore, pers. comm., Sept., 2003). In another incident, a 38 year-old woman was stung on the arm, with no systemic symptoms; her husband saw the jellyfish and a biologist familiar with *A. mordens* saw what he believed to be this species in the water shortly after (R. Hore, pers. comm., Oct., 2003).

Several explanations exist which may account for the differential symptoms. First, it is possible that a different species than *A. mordens* is responsible for the stings. This seems unlikely because the same species was recovered from multiple sting events with similar sting characteristics. Second, it is possible that different intensities of stings or different susceptibilities in the sting victims have led to very different outcomes. While differential susceptibilities and severities should not be ignored, it seems unlikely that these alone would fully explain the wide range of symptoms from

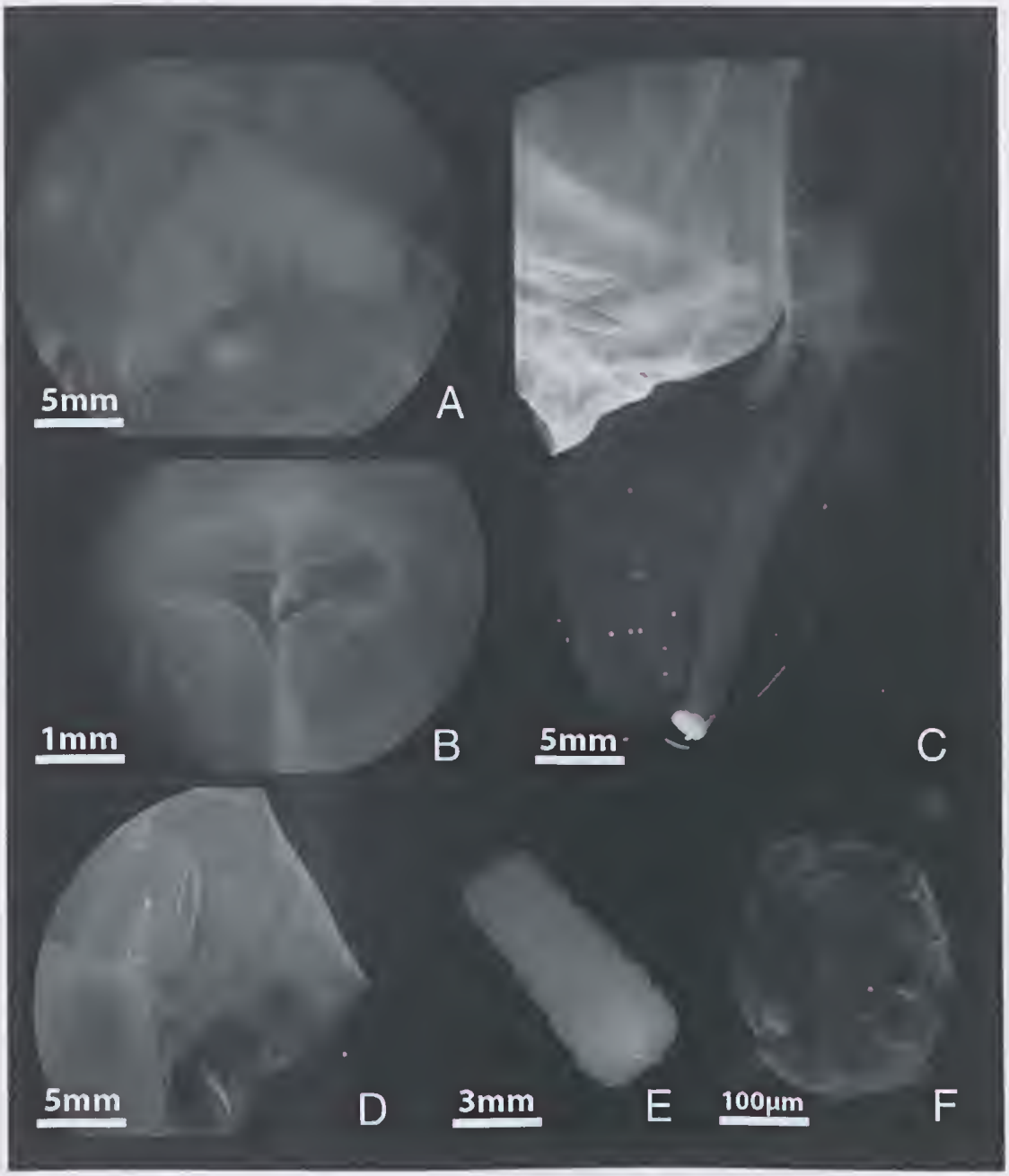


FIG. 2. *Alatina mordens* gen. et sp. nov. A, Crescentic phacellus with long cirri. B, Expanded lower covering scales, producing a T-shaped rhopalial niche. C, Pedalium, with greatly rounded adaxial keel. D, Velarial canals. E, Contracted tentacle, with regular constrictions. F, Statolith, dissected out of rhopalium; note that the statolith in this figure is orientated as it is in life, i.e., with the truncate border facing upward, whereas for inter-species comparison the truncate border is standardized to be the base.

mild to potentially lethal, all in previously healthy individuals. Third, it is possible that the medusae go through ontogenetic, seasonal, or reproductively-related changes in toxicity. No

data currently exist as to whether this is or is not the case, but it should be a priority for collaborative study by ecologists, toxinologists and taxonomists.

STING MANAGEMENT. A thorough treatment of stings and sting management is given by Williamson et al. (1996). When swimming in areas where cubozoans may occur, common-sense sting precautions should be employed, such as wearing protective clothing over exposed skin areas, e.g., a Lycra body suit. There is no medical or scientific evidence that commercial sting repellants or swimming like a turtle are effective methods of sting prevention. If stung, the best-known treatment for minimizing further envenomation is to pour vinegar liberally over the sting area for 30 seconds; this has been shown to be effective for a wide range of cubozoan stings (Williamson et al., 1996). If tentacles are present on the skin, they can then be safely removed. For severe stings, or those thought to be potential Irukandji envenomations, the patient should be made comfortable and medical treatment sought as quickly as possible.

There are many sources dispensing advice on jellyfish sting treatments, many of which are simply inaccurate. Contrary to popular belief, rubbing with sand or washing with freshwater often do more harm than good, causing additional nematocysts to discharge into the victim's skin. Methylated spirit is still often said to work well, but has been scientifically shown with *Chironex fleckeri* to cause immediate, massive discharge of nematocysts rather than to inhibit discharge (Hartwick et al., 1980); thus, it should not be used. There is also a common misbelief that vinegar stops the effect of the sting (i.e., relieves the pain, stops the illness) – this is untrue. It only disables undischarged nematocysts from discharging, eliminating further envenomation; vinegar should be used in all cases where stings from dangerous cubozoans are suspected.

There is no cause for alarm with the recognition of *A. mordens*. Most stings attributable to *A. mordens* occur at night, when the medusae are attracted to artificial lights (R. Hore, pers. comm., 2000; P. Colwell, pers. comm., 2000). Perhaps the most urgent action that should come from formally recognizing this species and its potential for harm, is the quest for an antivenom for severe cases of Irukandji syndrome. The only jellyfish antivenom that has been developed is for *Chironex fleckeri*, and this was shown by Fenner et al. (1986) to be ambiguous in managing Irukandji envenomation. Recent efforts to develop an antivenom to the Irukandji syndrome have been hampered by the sporadic occurrence of *Carukia barnesi*, combined with its small size (and thus, low venom yield per animal). *Alatina mordens* may provide a more stable subject, as it occurs all year and has a much larger, more robust body and tentacles, and thus more venom yield. However, *C. barnesi* and *A. mordens* do not appear to be closely related to one another, so the relationship between their venoms is unclear.

**Alatina rainensis** sp. nov.
(Figs 3, 4)

MATERIAL EXAMINED. HOLOTYPE: QMG55286, Raine Island, Great Barrier Reef, 11°35'34"S 144°02'12"E, Dec. 2002, collected by J. Seymour; gravid female, 17.78mm BH, 15.95mm DBW, 8.05mm IRW, 0.64mm TBW, 8.82mm PL, 4.29mm PW, 0.72mm CW.
PARATYPE: QMG55287, same locality as holotype; gravid female, 17.22mm BH, DBW not taken prior to sectioning, 7.93mm IRW, 0.58mm TBW, 8.68mm PL, 3.75mm PW, 0.68mm CW.

TYPE LOCALITY. Raine Island, outer Great Barrier Reef.

ETYMOLOGY. From Raine Island.

DIAGNOSIS. Body height at maturity small; gonads butterfly-form, attached in the central portion of the interradii only; phacellae with cirri rooted singly or in pairs.

DESCRIPTION OF HOLOTYPE. Bell taller than wide, with domed apex; with wide, shallow interradial furrows, lacking circum-aboral groove (Fig. 3A). Adradial furrows absent. Exumbrella sparsely sprinkled with minute unraised nematocyst freckles, absent on pedalia and velarium. Pedalia 4, interradial, with long stalk; inner keel quite rounded, outer keel more or less straight (Fig. 3B). Pedalial canals somewhat quadrate in cross section through stalk portion, flat through remainder; running along lower edge of pedalial lamella to about halfway, then leaving it perpendicularly, producing a 90° bend. Canal of fairly even width throughout length, bowing somewhat adaxially in a large shallow curve; straight at tentacle insertion. Tentacles 4, 1 per pedalium, round in cross section; straight-sided at the base. Tentacular banding pattern of two types: proximally, every 10th or 11th band smaller than others, thus giving tentacle a segmented appearance; distally, bands more or less alternate smaller with larger. Gonads butterfly-shaped, approximately ½ BH in length,

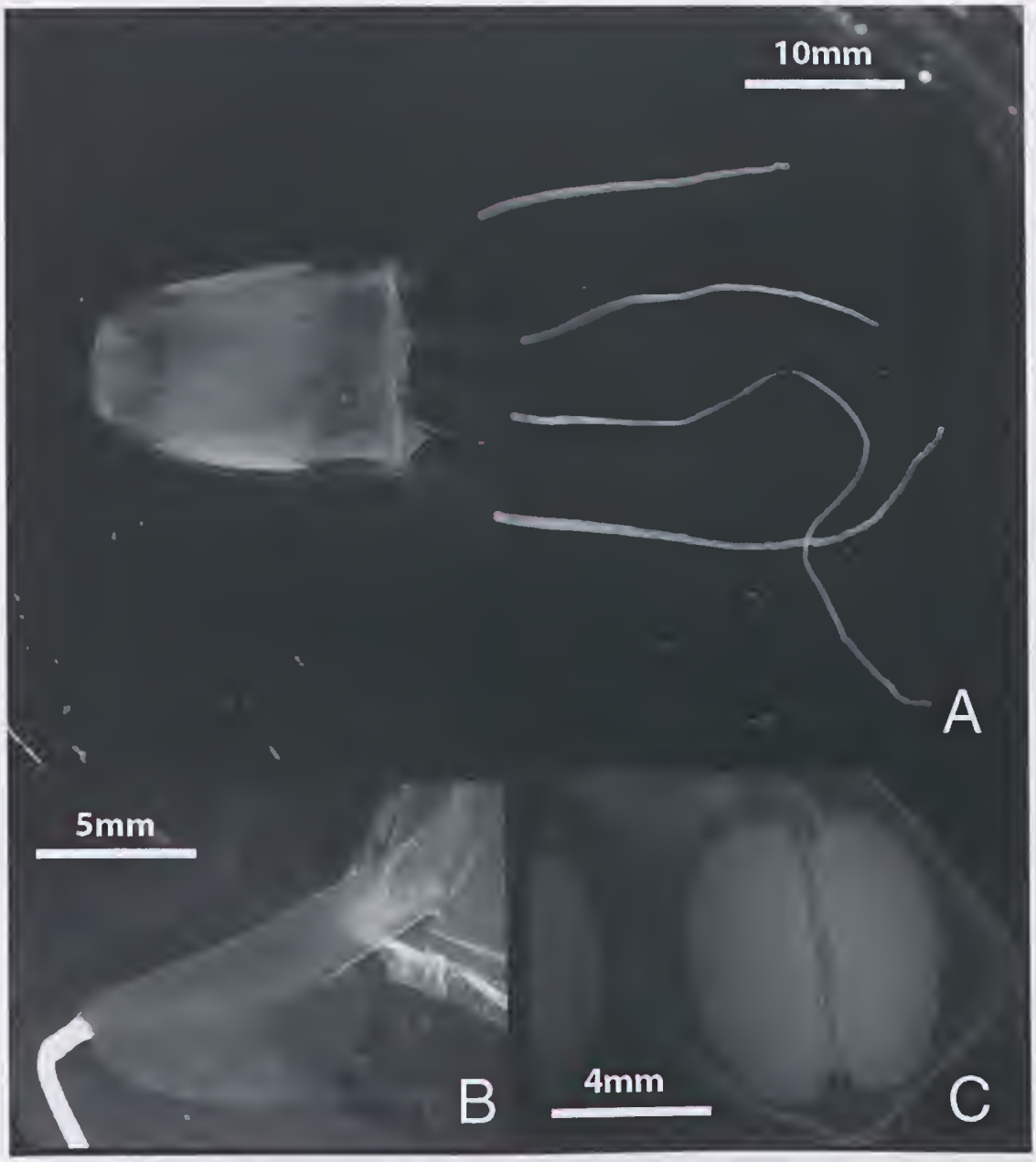


FIG. 3. *Alatina rainensis* sp. nov. A, holotype specimen, laying flat. B, Pedalium, with long stalk. C, Gonads, showing "butterfly" appearance.

but restricted to centre portions of interradii, approaching neither stomach nor pedalia, overlapping slightly at perradii; not pleated (Fig. 3C). Interradial septa with extremely minute perforations. Velarium narrow; with three canals per octant, simple throughout length (Fig. 4A). Perradial lappets lacking. Frenulae composed of a single narrow sheet of tissue, extending on to velarium nearly to margin. Rhopalial niche ostium T-shaped, with a shallow M-shaped covering scale above, and two shallow scales below, open at both sides between upper and

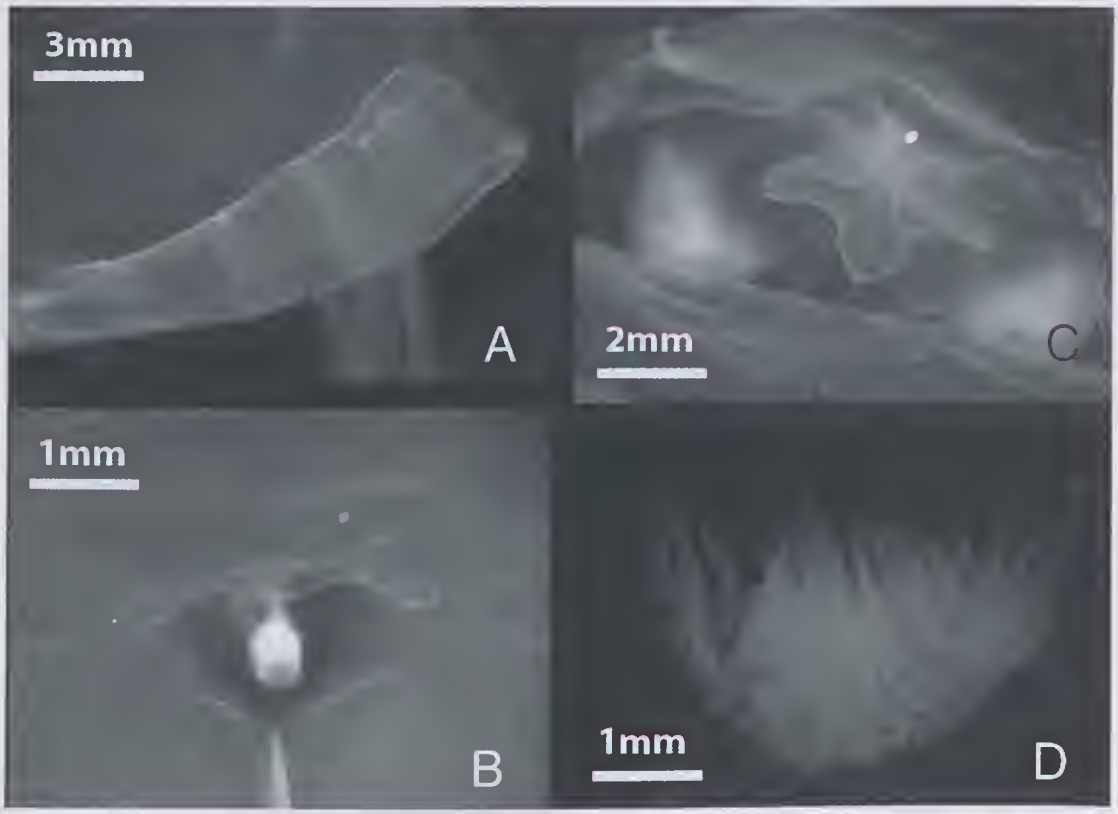


FIG. 4. *Alatina rainensis* sp. nov. A, Portion of velarium showing 3 simple canals per octant. B, Rhopaliar niche with W-shaped upper scale and poorly developed lower scales. C, Bell wall dissected away to show short, flat stomach. D, Phacellus, dissected out of stomach.

lower scales; lower scales separated by a deep furrow extending to velarium (Fig. 4B). Rhopaliar niche flush with exumbrellar wall; subumbrellar window bulging considerably. Rhopalia with 4 eyes, 2 median lensed eyes plus 2 elongate lateral eye spots. Lower of two lensed eyes large, round; upper laterally flattened into a strip distal to and cupping the lens. In preserved specimen, faint shadows occur where the 2nd pair of eye spots should be; thus, unknown whether eye spots faded or lacking. Statolith situated behind main eye, not below it; statolith shape indeterminable in preserved specimen. Rhopalial horns and warts lacking. Stomach small, shallow, completely lacking mesenteries (Fig. 4C). Manubrium very short, quadrate in cross section; mouth cruciform with 4 rounded lips. Gastric phacellae crescentic in interradii, opening toward midline; cirri approximately 50 per phacellus, long, simple, rooted singly or in pairs (Fig. 4D). Color in life not reported; preserved, the gonads, phacellae, and tentacles whitish, rhopalia dark brown, all other parts transparent and colourless.

CNIDOME (Fig. 7D-H; from holotype and paratype). The tentacular nematocysts are of two primary types and two very small secondary types. The largest are isorhizas, with a sub-spherical capsule and tightly packed tubule occupying the whole inside; the tubule morphology could not be determined due to lack of discharged capsules. The arithmetic mean of these undischarged capsules is 20.12x15.72μm (range 16.42-23.78μm long by 13.50-18.34μm wide, N=42; Fig. 7G). The other primary nematocysts are medium-sized microbasic curyteles, with a relatively narrow lemon-shaped capsule, with a distinct nipple at the distal end, and a distinctly visible shaft but poorly defined tubule; the arithmetic mean of these undischarged capsules is 17.37x11.51μm (range 14.99-19.70μm long by 10.43-13.11μm wide,

N= 37; Fig. 7E, undiseharged, Fig. 7F, diseharged). The seeondary nematoeysts inelude a smaller size elass of ovoid isorhizas (arithmetie mean 7.35x6.17μm, range 6.19-8.24μm long by 5.58-6.7μm wide, N=13; not figured) and a nearly spherieal type with a short, straight shaft and no visible tubule, presumed to be mierobasie amastigophores (arithmetie mean 6.84x6.40μm, range 6.19-7.16μm by 6.02-6.80μm, N=6; Fig. 7E).

The exumbrellar nematoeyst freekles have about 20-30 small spherieal isorhizas per eluster, with an arithmetie mean of 9.67 (range 9.22-10.47μm, N= 22; Fig. 7H). Other loose nematoeysts were found on a bell fragment from the apieal portion of the paratype's disseeted exumbrella; these ineluded large sub-spherieal isorhizas similar to those found on the tentaeles (mean of 21.89x17.89μm), mierobasie euryteles (16.55x13.01μm), and large subovate mierobasie p-mastigophores (mean of 28.28x 13.82μm). It is presumed that the isorhizas and euryteles were transferred from the tentaeles during instrument handling, but whether the mastigophores were even from this speeies is not known; this type of nematoeyst is eharaeteristie of several undeseribed speeies of Irukandjis. The nematoeysts of the gastrie eirri are extremely small euryteles, averaging 7.71 x 5.45μm (range 6.53-8.96μm long by 4.61- 6.55μm wide, N=24; Fig. 7D). Nematoeysts were not observed on the lips, despite exhaustive searehing.

VARIATION. The paratype differs from the holotype in the more strongly alternate tentaele banding pattern lacking the 10-band groupings.

DISTRIBUTION. The type loeality.

REMARKS. *A. rainensis* differs from all other earybdeids in its unique eombination of ereseentie phaeellae and butterfly-form gonads. The ereseentie phaeellae are typieally assoeiated with the *Alatina* group, but the butterfly-form gonads are typieally assoeiated with the distantly related *Tripedalia* group. However, this speeies does not appear to be an evolutionary intermediate between the two groups, beeause the rhopalial niehe ostia and windows, as well as the velarial eanals, are also of the *Alatina* form. Thus, the speeies seems elearly of *Alatina* affinity, and the odd gonad shape appears to be eonvergent.

**Alatina moseri** (Mayer, 1906) eomb. nov.
(Fig. 5A)

*Charybdea moseri* v*Mayer, 1906: 1135-1136, pl. 1, fig. 2-2c; n. sp., description and illustrations; Bigelow, 1909: 19-20; young stage of *C. grandis*; Bigelow, 1938: 144, junior synonym of *Carybdea alata*; Chu & Cutress, 1954: 9, cause of dermatitis, Hawaii; Kramp, 1961: 304; in synonymy of *Carybdea alata*.

*Carybdea moseri* Mayer, 1915: 171, probably young of *C. alata* var. *grandis*; Mayer, 1917: 189 [in part], fig. 3; only half-grown stage of *C. alata*.

*Carybdea alata* var. *moseri* Mayer, 1910: 512; probably a variety or young stage of *C. grandis*; probably identical with *C. philippina;* Light 1914: 196; = *C. philippina*, Philippines; Stiasny, 1919: 34, 37-38, fig. 5, Sumatra; Bigelow, 1938: 144, in synonymy of *C. alata*.

MATERIAL EXAMINED. SYNTYPE: USNM #21800, Str. Albatross, sta 3829, Avalu Pt., Lanai Island, Hawaii; 23 specimens; poor condition, uninterpretable.

OTHER MATERIAL EXAMINED: USNM #22311, Albatross Station 3931, from Honolulu to Laysauld, Hawaiian Islands, 2535 fathoms; 1 specimen in very fine condition, 39.43mm BH, 29.88mm DBW, 13.88mm IRW, 1.19mm TBW. USNM #29632, Albatross Station 3829, South coast of Molokai Island, Hawaii, 1 April 1902, at surface; 2 specimens in very fine condition, A) 85.37mm BH, 51.47mm DBW, 26.82mm IRW, 74.67mm AR, 1.47mm TBW, B) 73.34mm BH, 43.30mm DBW, 22.88mm IRW, 62.48mm AR, 1.87mm TBW (Fig. 5A).

TYPE LOCALITY. Avalu Pt., Lanai Island, Hawaii.

DIAGNOSIS. Nematoeysts present or absent on exumbrella and pedalia, laeking on velarium, with two median and two lateral eyes, with phaeellae eomprised of numerous eirri pairs, velarial eanals 3 per oetant and either simple or of two forms.

REVISED DESCRIPTION. Bell to about 85mm BH, 27mm wide, tall, narrow; with bluntly rounded apex, without eireumaboral groove; with thin but rigid body (Fig. 5A). Exumbrella laeking nematoeysts and warts in most speeimens. Interradial and adradial furrows laeking. Pedalia 4, approximately 1/4 BH, nearly as wide as long, with widely rounded adaxial keel and narrow abaxial keel. Pedalial eanals simple at bend; not flaring at tentaele insertion, flat throughout length. Tentaeles 4, simple, round in eross-section, with equal-sized nematoeyst rings; straight-sided at the base. Phaeellae in ereseentie rows at interradii; eirri long, arranged in parallel manner, rooted together in pairs. Mouth with 4 simple lips. Rhopalial niehe flush with exumbrella; T-shaped, with a single broadly rounded eovering seale above and two well developed seales below. Rhopalia with 2 round median eyes with lenses and 2 lateral, elongate

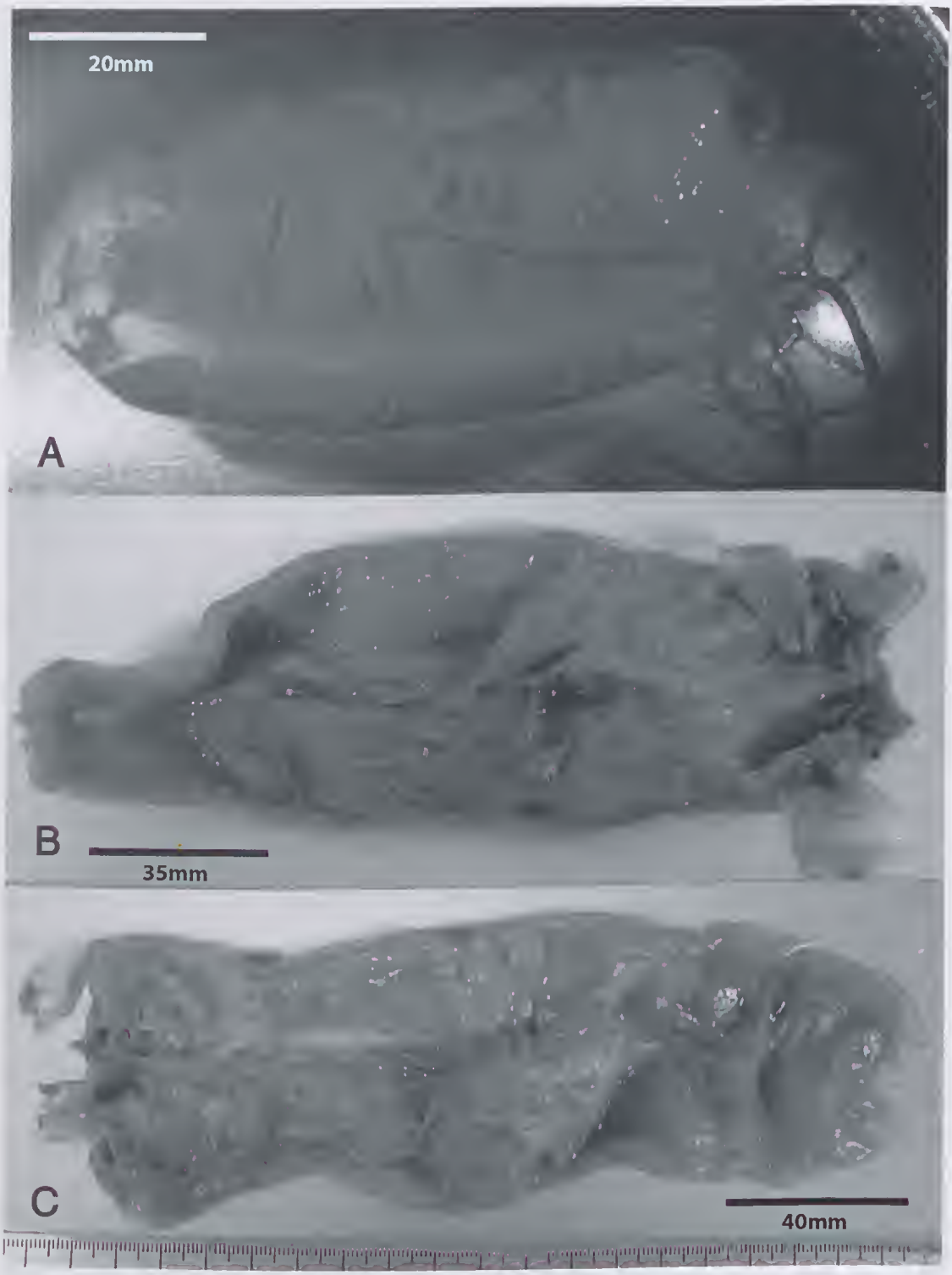


FIG. 5. *Alatina moseri* (Mayer, 1906) comb. nov., and *A.grandis* (Agassiz & Mayer, 1902) comb. nov. A, *A. moseri*, non-type specimen from Molokai Island (USNM 9632). B, (MCZ1043); C. (MCZ342). *A. grandis*, non-type specimens from the Hawaiian Islands, caught in 1861 and identified by Bigelow (1909:20).

eye spots slanting upward away from between the two median eyes. Statolith disintegrated, uninterpretable in preserved specimens. Rhopalial horns lacking. Velarium wide; nematocyst warts lacking. Velarial canals 3 per octant, simple and unbranched. Perradial lappets lacking. Frenulum very broadly webbed when viewed laterally, narrow and pointed along velarium; nearly reaching velarial edge. Gonads attached along entire length, reaching from stomach to level of rhopalia, not extending to pedalial canal. Interradial septa perforations lacking. Stomach wide and shallow. Mesenteries lacking. Color in life unknown; preserved body hyaline, tentacles pink, eye spots dark brown, gonads milky yellow.

VARIATION. USNM29632-A has nematocyst freckles in a single row of the outer pedalial keel, and also a few scattered upon the exumbrellar surface. Relationship of this specimen to others is not well understood. Velarial canals nearest the pedalia are biforked in USNM22311.

DISTRIBUTION. Hawaiian Islands.

REMARKS. Placed in *Alatina*, based on crescentic gastric phacellae, 3 velarial canals per octant, and broadly rounded abaxial pedalia wings. However, it may be distinguished from the other species by several characters. First, the gastric cirri are rooted in pairs, whereas in other forms they are typically rooted in bunches. Second, the velarial canals are straight and unbranched, similar to most species in the *alata*-group but differing from others such as *A. grandis* comb. nov. and at least two undescribed forms. Third, the rhopalia of *A. moseri* have only 4 eyes, 2 median eyes with lenses and 2 lateral ocelli. This feature was also described for immature specimens of *A. grandis* (Agassiz & Mayer, 1902). And indeed, several workers have thought that *A. moseri* is merely the young of *A. grandis* (Bigelow, 1909: 19; Bigelow, 1938: 138, 144-145; Mayer, 1910: 507, 512; Mayer, 1915: 171; Mayer, 1917: 189). However, *A. moseri* specimens have fully mature gonads, so they are unlikely to be the young of another species. Bigelow (1938: 138, 145) thought that *A. moseri* might be a dwarf race of *A. grandis*. There is limited value in recognizing races among diagnosably different forms.

Mayer (1906) thought this species might be the same as *Carybdea* sp. of Semper (1860: fig. 9) from the Philippines, subsequently named by Haeckel (1880) as *Procharybdis turricula*. Oddly enough, Mayer (1910: 512) and Stiasny (1919: 37) both confused Semper's and Haeckel's forms, attributing Haeckel's *C. philippina* to Semper's fig. 9, whereas Haeckel gave the name to Semper's fig. 8. To whichever one Mayer intended to refer, he (Mayer, 1910: 512) stated that *C. moseri* and Semper's form were "probably identical." Light (1914: 196) regarded the two species as identical. I have translated Haeckel's descriptions, and studied them and Semper's figures extensively; I am unable to find any characters that definitively characterize either of Semper's species, whereas *A. moseri* is diagnosable based on the peculiar paired phacellae bunches, having only four eyes, and the lack of exumbrellar nematocysts.

Unfortunately, there are some discrepancies between the reported station data and the data on the specimen labels; it is difficult to say with certainty what is accurate. First, station 3931 was not included in the published list, but was indicated on the label in Mayer's writing as being *Charybdea moseri* n. sp. Second, specimens from station 3829 are indicated on two samples, USNM29632 and 21800, unfortunately with different localities. Furthermore, the specimen numbers do not match those published. Specifically, Mayer listed 10 specimens from station 3829, collected 1-2 April at Avalu Point, Lanai Island. However, neither of the two lots of specimens is a match. USNM29632 matches the date, 1 April, but gives the locality as Molokai Island, and contains 2 specimens. USNM21800 matches the locality, Avalu Pt., Lanai Island, but there are 23 specimens. The remaining samples could not be found. Mayer (1906: 1136) indicated USNM21800 as type, which is unfortunate, since the specimens are now completely fragmented and uninterpretable. He indicated in handwriting on the specimen labels in USNM29632 that that lot was to be the type, but he did not indicate this in publication. Lots USNM29632 and 22311 are in excellent condition.

## OTHER NOMINAL SPECIES OF *ALATINA*

*Alatina alata* (Reynaud, 1830) comb. nov., is completely unrecognizable based on the original description and illustration, but because of the prevalence of the name in the literature, should be stabilized by declaration of a neotype; a full redescription of a South Atlantic specimen will serve as the basis for identification of the taxon in the future. Accordingly, an application to the

ICZN to conserve *A.alata* will be submitted as soon as a suitable neotype is located.

*Alatina obeliscus* (Haeckel, 1880) comb. nov., seems to fall within the *Alatina* group, based on its large phacellae. However, its exact identity with respect to its congeners cannot be determined. Even with a specimen to study, it is unlikely that the species could be properly diagnosed, based on its uneven development of the velarial canals, and the size of Haeckel's specimen (35mm BH, 20mm BW), both of which indicate that it was very likely a juvenile. Assuming it is one of the branched-canal species, it would be relatively easy to diagnose, but only with mature specimens. Haeckel described a "button-form" thickening at the end of the tentacles. This is found occasionally in specimens that have spent too long in captivity in sub-optimal conditions (e.g., too warm, too confined, poor circulation; Gershwin, unpubl. data), and does not appear to be a diagnostic species character. Because this species is unlikely to be recognizable under any circumstances, the name is best abandoned.

*Alatina philippina* (Haeckel, 1880) comb. nov., was described based on a line drawing by Semper (1860, pl. 39, fig. 8). At a mature bell height of 30mm, one might expect that the species would be diagnosable, but Semper's line drawing and Haeckel's description are too vague to allow for differentiation of this species from any other. It seems closest to *A. tetraptera* (Haeckel, 1880) comb. nov., based on the long pedalia and wing-like phacellae. However, whether the two are synonymous or not cannot be concluded from available information. Thus, in the interest of stability, it seems most conservative to abandon the name.

*Alatina pyramis* (Haeckel, 1880) comb. nov., appears distinctive based on features from Haeckel's (1880) description and illustrations. First, being only 30mm tall and having full gonads, the only other *Alatina* spp. in this adult size range would be *A. rainensis* sp. nov., which has butterfly-shaped gonads, and *A. tetraptera*, which has peculiarly long pedalia and wing-shaped phacellae. Second, *A. pyramis* is the only species with frizzy lips. Third, the pedalia are considerably narrower than is typically found in other species of *Alatina*. I have no doubt that when this species is encountered again, it will be immediately recognizable based on these combined characteristics.

*Alatina tetraptera* (Haeckel, 1880) comb. nov., seems to fall within the *Alatina* group, based on the large pedalia with "mighty" wings and the phacellae with long cirri. Furthermore, the rhopalial niche ostia were described as "heart-shape," which could be easily mistaken for T-shaped if the specimen were not well preserved. Finally, only a single large eye was observed on the rhopalia, which is characteristic of some *Alatina* spp. Haeckel classified this species into *Procharybdis*, based on the absence of the velarial canals and frenulum. I am unsure what to interpret from the missing velarial structures, but it would be wrong to regard the species as anything other than distinct based on the split, wing-like phacellae (Haeckel, 1880: pl. 25, fig. 4) and the extremely long, uniquely shaped pedalia (pl. 25, fig. 3). These two characters are not known in any other cubozoan, except possibly the later-described *A. pyramis*. This species has not been recognized in the scientific literature for almost 100 years, but it seems appropriate to revalidate it awaiting fresh material that can be studied for a proper redescription. At a mature bell height of 30mm, with the structures described, I think this species would be recognizable if found again.

*Alatina turricula* (Haeckel, 1880) comb. nov., described from a line drawing by Semper (1860, pl. 39, fig. 9), is unrecognizable. It is clear from the widely rounded pedalia in the original illustration that this medusa is a member of the *Alatina* group. Furthermore, due to its extremely tall body (170mm), it is possible that it is referable to *A. grandis*. However, this is merely speculation, as it is impossible to diagnose with certainty from the drawing and vague description. There are no structural characters described that would serve to differentiate this species from any of the others; thus, it seems most conservative to permanently abandon the name.

*Alatina grandis* (Agassiz & Mayer, 1902) comb. nov.: The type material of this species from the Paumotus, has apparently been lost; neither MCZ nor USNM know of its whereabouts. Specimens from the Society Islands (MCZ1043 and MCZ 342), identified by H. Bigelow as *C. grandis*, match the original description but are too poorly preserved to be usefully interpretable. One (MCZ 342, BH 170.93, DBW 57.78, IRW 33.56+), bears the following collection data: Pacific Ocean, Society Islands, coll. A. Garrett, 29.ix.1861; originally preserved in alcohol, now preserved in formalin (Fig. 5C). The other (MCZ

1043, BH 184.55, DBW 59.55, IRW 33.18), was apparently collected at the same time, and delivered to the MCZ by A. Garrett in 1864 (Fig. 5B). The species seems distinctive based on its extremely large size, and in having only one median eye and short, branched velarial canals.

*Alatina madraspatana* (Menon, 1930) comb. nov., is described as having up to 5 branched velarial canals per octant, an apical concavity, and 6 eyes on each rhopalium, one of the median bearing a lens. This combination of characters is unique, and thus, the species is regarded herein as valid. However, I remain curious about the velarial interpretation, as it seems rather odd for an *Alatina* to have 5 velarial canals per octant.

**Manokia** Southcott, 1967

**Manokia stiasnyi** (Bigelow, 1938)
(Fig. 6)

*Charybdea* spec. v*Stiasny, 1930: 3-5, figs 1-7; occurrence in New Guinea, and description of species; Stiasny, 1937: 216; brief comparison of branched tentacles.

*Carybdea stiasnyi* v*Bigelow, 1938: 136; sp. nov., in reference to Stiasny's (1930) description; Kramp, 1961: 306; Southcott, 1963: 51; tentacle comparison; Kramp, 1968: 69 [doubtful species].

*Manokia stiasnyi* Southcott, 1967: 667; new genus comb. nov.

*Charybdea stiasnyi* vPayne, 1960: 6, 28, 32-33.

MATERIAL EXAMINED. HOLOTYPE: IRSNB IG 9223, Manokwari, New Guinea, 10 March 1929; male, 23.59mm BH, 20.11mm DBW at the top of the pedalium, 21.66mm DBW at the widest point, 10.24mm IRW, 1.32mm TBW, 12.52mm Pedalial length, 2.23mm pedalial width at widest part.

TYPE LOCALITY. Manokwari, New Guinea.

REVISED DESCRIPTION. Body barrel-shaped, widest in middle region, with conspicuous apical depression (Fig. 6A). Interradial furrows deep, nearly meeting pedalia. Adradial furrows deep, demarcating rhopaliar region and interradial thickenings. Bell with scattered gelatinous nematocyst warts, extending onto velarium but warts not specific to any canal or pattern. Pedalia 4, interradial, scalpel-shaped, with relatively narrow inner keel, lacking nematocyst warts or freckles. Pedalial canals flat throughout length, with slight upward-pointing nub projecting into sub-lamellar space; straight at tentacle insertion. Tentacles 4, interradial, round in cross section, with evenly-sized nematocyst bands. Nematocyst bands drawn out adaxially into short, blunt extensions, approximately 8 per tentacle (Fig. 6B); one tentacle having extensions in 2 alternating rows, other tentacles having them

FIG. 6. *Manokia stiasnyi* (Bigelow, 1938). A, holotype specimen. B, One tentacle, showing peculiar branching pattern. C, Subumbrellar view of rhopalium, with convex windows.

in more or less a single row. Rhopaliar niche flush with surrounding bell wall; with T-shaped ostia, comprised of a single thickened covering scale above and two well developed covering scales below. Upper scale with a median flap hanging down into ostium in front of rhopalium. Rhopalial horns absent. Subumbrellar wall of rhopalial niche made of a thick window of un-muscled mesoglea, hemispherically convex on subumbrellar side, concave on rhopaliar niche side (Fig. 6C). Rhopalia with two median lensed eyes, distal-most larger than proximal, and two pairs of unevenly sized lateral eye spots, distal pair larger than proximal pair. Phacellae crescentic, with numerous long cirri, arranged more or less parallel; number of trunks in each phacellus indeterminable without damaging specimen, but appears to be between 5 and 10. Stomach shallow, with short manubrium; specimen with large amphipod high inside the subumbrellar cavity. Mouth shape indeterminable without damaging specimen. Mesenteries lacking. Frenulae well developed,

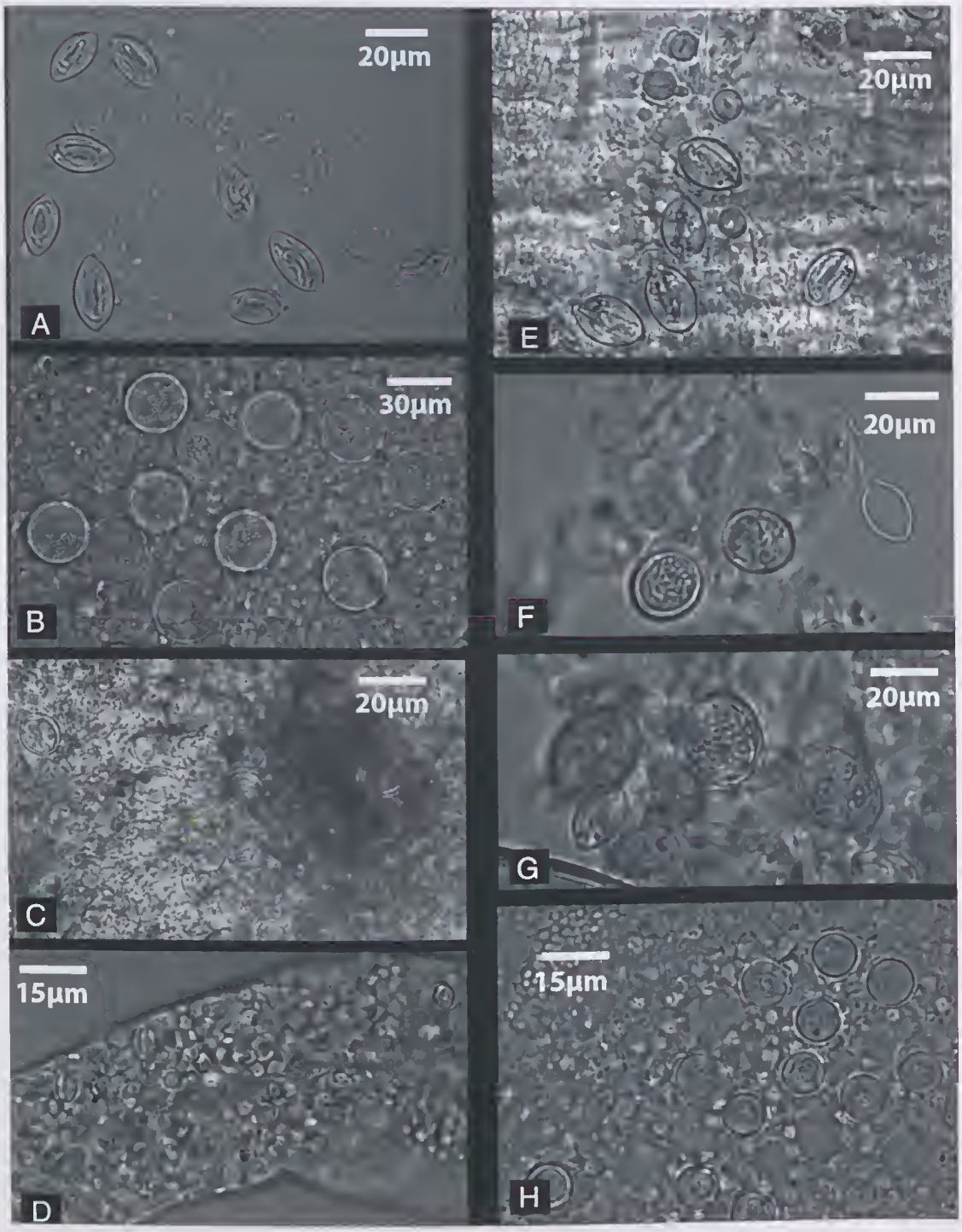


FIG. 7. Nematocysts of Alatinidae. A, *A. mordens*, tentacle. B, *A. mordens*, bell wart. C, *M. stiasnyi*, tentacle. D, *A. rainensis*, gastric cirrus. E-G, *A. rainensis*, tentacle. H, *A. rainensis*, bell wart. See text for complete descriptions and measurements.

but short, reaching only approximately halfway to velarial margin. Perradial lappets absent. Velarium 2.71mm wide, with 4 undulating, unbranched canals per octant. Gonads leaf-like, attached along nearly whole length of interradial septa, projecting laterally into coelenterie cavity. Colour in life unknown.

CNIDOME (Fig. 7C). The tentacles of *Manokia stiasnyi* have a monocnidome of sub-spherical eurytele with a thick capsule wall, with an arithmetic mean of 15.23μm long by 12.43μm wide (range 13.42-16.53μm long by 11.54-13.63μm wide, N=12). Nematocysts from other parts of the body were not examined due to brittleness of the specimen.

REMARKS. Stiasny (1930) commented that the exumbrella of this species was smooth, lacking nettle-warts. However, this is inaccurate. The holotype specimen has a few scattered warts, and while most of these have become flattened through the passage of time, several are still raised. I could not observe any particular pattern to their arrangement, but they are present on the velarium as well as the body.

The tentacles are worthy of discussion, as they have always been the chief character used to separate this species from others. The tentacles are typically said to be branched (Stiasny, 1930; Bigelow, 1938; Kramp, 1961; Southcott, 1967). However, the tentacles are not branched in the conventional sense, and referring to them as such is somewhat misleading. In branched tentacles, one would expect that the central lumen would be branched, in order to maintain the flow of nutrients and various fluids. However, in the tentacles of the present specimen, it is the nematocyst bands that are branched rather than the tentacle itself. Therefore, the "branches" are not true branches, but rather, merely elongations of one side of the tentacular nematocyst bands. Each band is drawn out a short distance adaxially like a little tail, with these extensions primarily arranged in two vertical rows. This character is somewhat reminiscent of the neckerchief-shaped tentacle bands of *Carukia barnesi*, but the resemblance is apparently only superficial. In *M. stiasnyi*, the bands are apparently normal around most of the tentacle, and only extended in a bluntly rounded, almost herniated manner along the adaxes. In *C. barnesi*, the bands are widely spaced, and the adaxial extensions are quite remarkably triangular in form, extending distally.

The peculiar branching of the tentacles led Stiasny (1937: footnote p216) to think that the medusa might be the young of an unusual chirodropid he identified as *Chiropsalmus quadrigatus*. His specimen from the Maldives had numerous filaments on the tips of the tentacles. He misunderstood Mayer's (1910) redescription of *C. quadrigatus*, thinking that each pedalial finger should bear numerous tentacles, rather than a single one. In fact, *M. stiasnyi* bears no resemblance whatsoever to *C. quadrigatus*, nor does Stiasny's Maldivian specimen; the latter will be formally described in a forthcoming chirodropid revision.

Two particular characters suggest a strong affinity to the *Alatina* species group, namely, the T-shaped rhopaliar niche ostia and the crescentic-shaped phacellae of long cirri. Although similar, the ostia are also quite different, in that the upper covering scale has a central flap that hangs down, rather than the typical straight scale of *Alatina*. The two lower covering scales are quite robust, and the indentation between them extends down to the velarium.

Southcott (1967) erected *Manokia* based on the branched tentacles, 4 undulating velarial canals per octant, and horizontal phacellae. He commented that the branched tentacles alone would be insufficient basis to establish a new genus, because they could simply be aberrant; however, the velarial canals were quite distinct. He went on to compare the canals with those of *Carybdea rastonii* and *C. marsupialis*, citing that those of *M. stiasnyi* are more numerous but simpler in nature. However, any species in the *Alatina* group would have been a closer comparison (though *M. stiasnyi* still would have proven unique). The crescentic phacellae and T-shaped rhopalial niche ostia are more reminiscent of *Alatina*, as are the more or less simple velarial canals and lack of mesenteries.

Kramp (1968) remarked that Bigelow's species was doubtful, but did not elaborate why. Less than a decade earlier, he had considered it valid (1961). The point is moot anyway, for re-examination of the specimen has revealed a combination of characters unlike those of any other known species.

## GENERAL DISCUSSION

The species of the *Alatina* group all share the conspicuous characters of crescentic phacellae and T-shaped rhopaliar niches. However, the

internal and external relationships of this group have been debated in the past. Traditionally, *C. alata* auct. was diagnosed by focussing on the crescentic phacellae, with varieties sometimes based on size differenees (Mayer, 1910; Kramp, 1961). Other characters occasionally used for diagnosis have been inconsistent and often misinterpreted, for example, rhopaliar niche shape (Mianzan & Cornelius, 1999). However, Gershwin (2001) and Gershwin & Collins (2002) showed that analysis of numerous charaeters in jellyfishes ean highlight relationships that were previously overlooked with narrower analyses. Numerous forms of *Carybdea alata* from disparate loeations, all with crescentie phacellae, differ with regard to umbrellar and velar nematocysts, number and degree of branching of the velarial canals, number of eyes, number of phaeellae roots, shape of the rhopaliar niche ostium seales, and tentaele banding patterns. No doubt additional differences will be found with closer morphological study, cnidome comparison, and molecular analysis of these and other forms.

Within the *Alatina* clade, the most attention historically has fallen on the interpretation of *Alatina grandis*. According to Bigelow (1938), *C. grandis* was the first in the group to be positively identifiable, because *C. alata* as described by Reynaud (1830) is unrecognizable and the name was revived by Vanhöffen (1908) for stability. Unfortunately, Vanhöffen failed to assign a particular specimen or suite of characters to the name; thus, we are left with the name of an unrecognizable species, and stability was not served. Bigelow went on to conclude that all the forms within the *C. alata* group are but one species, with *C. grandis* being the adult form. However, three decades earlier, Bigelow (1909) thought that *C. grandis* was valid and that the Paeifie complex of *C. philippina*, *C. grandis*, and *C. moseri* could be easily separated as follows: *C. philippina* matures at only 30mm BH, whereas *C. moseri* does not begin to develop gonads until 60mm BH; *C. moseri*, in turn is elosely allied with *C. grandis*, being separable, if at all, on the velarial canals being simple in the former, branched in the latter. More often than not, *C. grandis* has been interpreted as a gigantic variety of *C. alata* (Mayer, 1910, 1915, 1917; Light, 1921; Thiel, 1928), although Kramp (1961), without comment, regarded *C. grandis* and all the nominal speeies in the group as junior synonyms of *C. alata*.

While most authors have argued over which crescentic-phacellaed forms should be considered species and which should be considered varieties, *alata* also became the subjeet of a large and confusing misunderstanding that spanned 14 deeades and never was completely resolved. Agassiz (1862) assigned Reynaud's *C. alata* to *Tamoya*, rather than to his *Marsupialis*, for reasons that are wholly unclear. *Tamoya haplonema*, the type species, could not possibly be eonfused with *C. alata* under any reasonable circumstances. Haeekel (1880) moved it baek to *Carybdea*, a combination which has been widely adopted since. However, Uchida (1929) identified his loeal large carybdeid as *Tamoya alata*. It is elear from his illustrations how he arrived at the *Tamoya* part of his identification, but there is no indication of how he eame to think that they were *alata*. His medusae were not *alata*-like in the sense of the crescentie phacellae and T-shaped rhopalial niehe ostia. He further misidentified the small species *C. sivickisi* to be the young of his *T. alata*; in faet, *C. sivickisi* shares only the erudest resemblance to any *Alatina*, in that both have 4 tentacles. All other characters, from the rhopalial niche ostia to the phacellae, from the velarial canals to the pedalia, are quite different. Over 40 years later Uchida remained confused on *Carybdea alata*, for he erroneously assigned to this speeies a single specimen from Cape Town with *C. marsupialis*-type gastric phaeellae and *T. haplonema*-like rhopaliar niche ostia (Uchida, 1970). Apparently Uchida's error was what led Branch and his eolleagues (1994) to erroneously identify the common Cape Town carybdeid as *C. alata*, and Pagès et al. (1992) to identify it as *T. haplonema*, when it should have been recognized as a new species (Gibbons & Gershwin, unpubl. data).

In the proeess of sorting out which of the *Alatina* speeies should be retained and which are unrecognizable, many other new species are likely to be found. For example, a single Indonesian specimen (SAMH967) from the Te Vega Expedition, and specimens from Sri Lanka (QMG317054, G317055) and Madagascar (QM G317053), all match the standard deseriptions for *C. alata* auct. but differ in numerous other structural eharacters. Sorting out the true biodiversity of the *Alatina* group will require fine feature study of a large number of speeimens from regions throughout the world's tropics.

Removal of several speeies from *Carybdea* and the Carybdeidae, in particular the well published

*C. alata* auct. and the obscure *M. stiasnyi*, in effect redefines both *Carybdea* and the Carybdeidae. I thus propose the following revised descriptions, pending a comprehensive revision. I am further excluding *C. sivickisi* from *Carybdea*, and the Irukandjis and *Tamoya* from the Carybdeidae, based on overwhelming morphological and molecular comparison; the full explanation and reclassification for these exclusions is beyond the scope of this paper, but is forthcoming (Gershwin, unpubl. data).

Carybdeidae. Carybdeida with gastric phacellae; with poorly defined rhopaliar niche covering scales; with nematocyst clusters on the pedalia; with unbranched tentacles.

*Carybdea*. Carybdeidae with epaulette-shaped or linear phacellae, comprised of short gastric cirri; with heart-shaped rhopaliar niche ostia; with usually two, sometimes 3-4, dendritically branched velarial canals per octant; with scalpel-shaped pedalia, typically with nematocyst clusters on the outer keel.

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**THE TYPE LOCALITY OF THE SPHAGNUM FROG *Philoria loveridgei* (ANURA: MYOBATRACHIDAE).**

*Memoirs of the Queensland Museum 51(2): 524. 2005:-* The Sphagnum Frogs (*Philoria*) of N NSW and SE Qld (*Kyarranus* of some authors) were revised by Knowles et al. (2004). Using allozyme and mitochondrial nucleotide sequence data supported by multivariate morphological analyses, they recognised 5allopatric species (2 new.

Their multivariate morphological analyses identified the holotype of *P. loveridgei* Parker, 1940 within the range of variation of *P. richmondensis* Knowles et al., 2004 and considered the former's stated type locality "McPherson Range, 3-4000 ft., S. Queensland" (Parker, 1940) to be sufficiently imprecise that it could be anywhere within the extent of either species. Without genetic data from the holotype or a more precise type locality, and recognising that their multivariate analyses did not completely separate the two species, they maintained nomenclatural stability by continuing with *P. loveridgei* for populations to which the name had "been traditionally applied" (Knowles et al., 2004:65), the taxon from the Border Ranges (although *P. loveridgei* has at various times been considered to include more distant populations now regarded as different taxa; e.g., Heatwole et al., 1995; Cogger, 2000; Anstis, 2002).

Parker (1940) did not indicate a collector or date of collection for the holotype but did provide a chain of evidence, apparently overlooked by Knowles et al. (2004), that associates the holotype with Philip Jackson Darlington, with Lamington National Park, and with further specimens from the type locality.

Parker noted that the holotype (Natural History Museum, London 1947.2.1994) was derived from a series previously reported by Loveridge (1935) as *P. frosti* (now known to be restricted to Mt Baw Baw, Victoria). Loveridge (1935) reported 6 specimens of *P. frosti* (18423-25) in the Museum of Comparative Zoology, Harvard University from "MacPherson Range, Q" collected by P.J. Darlington in 1932. In his papers on the Australian amphibian and reptile collections in the MCZ, Loveridge (1934, 1935) noted that Darlington visited Australia on the 1931 Harvard collecting expedition, and continued to collect in E Australia, from Sydney to Cape York, in 1932.

Loveridge (1934, 1935) reported 1 reptile species and 3 amphibians in the MCZ, from the MacPherson Ranges by Darlington in 1932: 9 specimens of the skink *Eulamprus tryoni* (as *Sphenomorphus tryoni*) from 3,000-4,000ft (Loveridge, 1934), the 6 *Philoria* specimens, 11 *Litoria caerulea* (as *Hyla caerulea*) and 3 types of *Crinia darlingtoni* Loveridge 1933 (now *Assa darlingtoni*), stated by Loveridge (1935) as being from "National Park, Q." In his description of the latter, Loveridge (1933) gave the type locality as "between 3,000 and 4,000 feet in the Queensland National Park, MacPherson Range, Queensland, collected by Dr. P.J. Darlington, March 10-16, 1932". Darlington (1953) described a carabid beetle, *Setalis sloanei*, from his 1932 collections. The label on the holotype states "Nat. Park, Q. McPherson Rge Mar. 1932 3-4000ft. Australia Harvard Exp. Darlington" (P.D. Perkins, pers. comm.).

While I have been unable to trace diaries for Darlington's 1931-32 visit (J. Rosado, B.D. Farrell, P.D. Perkins, pers. comm.), it is apparent that his visit to the MacPherson Ranges was via Lamington National Park, declared in 1915, and often referred to in the literature of the time as "the National Park" (Jarrott, 1976, 1990). Not only is there clear evidence that Darlington collected the *Assa darlingtoni* and *Setalis sloanei* types in Lamington National Park, but *Eulamprus tryoni* is not known to occur further west in the MacPherson Ranges than Lamington National Park (Sadlier, 1998).

It is likely that when visiting Lamington National Park, Darlington accessed the area from O'Reilly's Guest House, opened in 1926 and the only regular point of access to the National Park in March 1932. Access at the time was via Lahey's Road, ascending the Cainbable Range from Stockyard Creek, a trip taking several hours along a track mostly travelled by horse (Jarrott, 1990).

Other localities visited by Darlington in 1932 are (S to N): National Park [= Royal National Park], Megalong Valley, Blackheath, Hartley Vale, Mt Wilson, Salisbury, Barrington Tops, Dorrigo, Cascade (NSW), Vine Creek, Ravenshoe, Millaa Millaa, Lake Barrine, Mt Carbine, Mt Spurgeon, Port Stewart, Coen, Lankelly Creek, and Rocky Scrub (Qld) (Loveridge, 1934, 1935). None of these are near Lamington National Park.

Without evidence that Darlington collected in the MacPherson Ranges other than in Lamington National Park, and recognising a lack of access tracks between Lamington National Park and the Richmond Range (known distribution of *P. richmondensis*), I consider the type of *P. loveridgei* was collected in Lamington National Park, within the known range of the species, and not within the distribution of *P. richmondensis*. Topotype material of *P. loveridgei* may confirm the identity of the typical population.

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# FIRST RECORDS OF THE FALSE CATSHARK, *PSEUDOTRIAKIS MICRODON* CAPELLO, 1868, FROM THE WATERS OF EASTERN AUSTRALIA AND INDONESIA

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Kyne, P.M., Johnson, J.W., White, W.T. & Bennett, M.B. 2005 12 31: First records of the false catshark, *Pseudotriakis microdon* Capello, 1868, from the waters of eastern Australia and Indonesia. *Memoirs of the Queensland Museum* **51**(2): 525-530. Brisbane. ISSN 0079-8835.

A new specimen of a rare deepwater chondrichthyan, the false catshark *Pseudotriakis microdon* Capello, 1868 is documented from the Coral Sea. This represents the first record of the species from off the east coast of Australia and only the second from Australian waters. The specimen, a 277cm total length (TL) mature male, was captured by exploratory deepwater dropline at a depth of 350m on 03/02/2004. Morphometrics are presented and compared to other published accounts. A further individual, a 287cm TL mature female captured by bottom longline operating at depths of 100–150m around Sawu, Dana and Raijua Islands, southeastern Indonesia, is documented from fish landing sites in Lombok, Indonesia. This individual was not retained and only its sex, maturity and TL were recorded. It represents the first record of *P. microdon* for Indonesia and for the northeast Indian Ocean. These specimens increase the known range of this rare, sporadically recorded, but widely distributed chondrichthyan. □ *Carcharhiniformes, Pseudotriakidae, Queensland waters, Indonesia.*

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The false catshark *Pseudotriakis microdon* Capello, 1868 (Carcharhiniformes: Pseudotriakidae) is a possibly cosmopolitan deepwater elasmobranch, however, it is sporadically recorded and its complete distribution remains unclear. The false catshark is benthic, primarily on the continental and insular slopes at depths of 200-1,900m, but can occasionally occur on the continental shelf (Bigelow & Schroeder, 1948; Compagno, 1984; Baranes, 2003). Most records are from the Northern Hemisphere, and the species appears to be rarer, or more rarely encountered, in the Southern Hemisphere. It has previously been recorded from the northwest Atlantic, off Canada (Gilhen & Coad, 1999) and New York to New Jersey (Bigelow & Schroeder, 1948); northeast and eastern central Atlantic from the Atlantic slope off Iceland, France, Portugal, Madeira, Azores to Senegal and the Cape Verde Islands (see Compagno, 1984; 1988); western Indian, Aldabra Island, Cosmoledo Island and Geyser Reef (Forster et al., 1970) and the Amirantes Islands, Seychelles (Baranes, 2003); eastern Indian, off Cape Leeuwin, Western Australia (Allen & Cowan, 1995); central Pacific, Hawaiian Islands (Crow et al., 1996); northwest Pacific, various localities off Japan from Honshu to Okinawa Islands (Jordan & Snyder, 1904; Taniuchi et al., 1984; Yano, 1992) and Taiwan (see Chen, 1963); and, southwest Pacific, Three Kings Ridge, Challenger Plateau and Hikurangi Trough (east of Mahia Peninsula) New Zealand (Stewart & Clark, 1988; Yano, 1992; Stewart, 2000). The species has not been recorded from either the southern Atlantic or the eastern Pacific, and it is most likely that it is more widely distributed than presently documented.

*Pseudotriakis* Capello, 1868 is a monospecific genus, characterised by its large adult size, soft-body, cat-like eyes and nictitating eyelids, large spiracles, wide angular mouth extending posterior to the eye, two large spineless dorsal fins, the first low, extended and keel-like, an anal fin, numerous extremely small cuspidate teeth (≥200 rows in each jaw), no precaudal pits, and an asymmetrical caudal fin (Compagno, 1984; 1988). Jordan & Snyder (1904) recognised *Pseudotriakis acrales* (from the Atlantic) as distinct from *P. microdon* (from the Pacific) however numerous authors (see Compagno, 1988 for an account) could not find any characters to reliably separate the two species and

FIG. 1. *Pseudotriakis microdon* QM I.34963. Lateral view of whole specimen. The first dorsal fin is not visible in the photograph. (Photo: Jeff Wright).

tentatively placed *P. acrales* in synonymy with *P. microdon*. Yano & Musick (1992) confirmed this synonymy with morphometric analysis, concluding that characters used to separate the species change allometrically as suggested by Compagno (1988). The Pseudotriakidae also includes *Gollum* Compagno, 1973; the two genera being readily distinguished by the height of the first dorsal fin. In *Gollum* the first dorsal fin is about the same size as, and is roughly equal in height to, the second dorsal fin (Compagno, 1973), whilst in *Pseudotriakis* the low, keel-like first dorsal fin is much lower than the second dorsal fin. *Gollum attenuatus* (Garrick, 1954), the sole member of the genus, is endemic to New Zealand (Compagno, 1988).

Here we present the first record of *P. microdon* from the east coast of Australia and the second known specimen from Australian waters, together with the first record from Indonesia and the northeast Indian Ocean.

## METHODS

The Australian specimen was frozen and transported to the Queensland Museum where it was examined prior to being fixed in formalin. Eighty-five morphometrics were recorded for the new specimen, including the 56 measurements presented in Yano & Musick (1992). Abbreviations and methods for measurements follow Compagno (2001), except those for the first dorsal fin length (D1L) and first dorsal fin base length (D1B) which follow that of Yano & Musick (1992). Morphometrics were compared with those given in Yano & Musick (1992). The following abbreviations are used for institutions: QM, Queensland Museum, Brisbane; WAM, Western Australian Museum, Perth.

The Indonesian individual was observed during surveys of the chondrichthyan catches at the fish landing site of Tanjung Luar on the eastern side of the island of Lombok in southeastern Indonesia. Sex, maturity and TL were recorded, but no morphometric measurements were taken and the specimen was not retained due to the remote location of the find.

## RESULTS

A 277cm TL mature male *P. microdon* (QM I.34963) (Fig. 1) was captured by deepwater multi-hook demersal dropline off the southwest side of Calder Reef, Coral Sea (~20°51' S, 153°13' E) at 350m depth on 03/02/2004. The individual was taken by an exploratory commercial fishing vessel targeting a broad range of deepwater reef fishes including flame and ruby snapper (*Etelis* spp.) and bar cod (*Epinephelus* spp.). Table 1 presents morphometrics for the Australian specimen, as well as the range of values for the 56 measurements given in Yano & Musick (1992).

A 287cm TL mature female *P. microdon* (Fig. 2) was observed and photographed at the fish landing site of Tanjung Luar on the eastern side of the island of Lombok, southeastern Indonesia on 08/09/2004 by a joint Australian-Indonesian team conducting fish market surveys. The individual was captured by demersal longline fishers targeting sharks (*e.g.* large carcharhinids and *Hexanchus griseus* (Bonnaterre, 1788)). No precise locality data was obtained, however the fishers are known to operate only around the

TABLE 1 (facing). *Pseudotriakis microdon* QM 134963, 2770mm TL. Proportional dimensions as percentages of total length, with comparison to values given in Yano & Musick (1992) where appropriate. Abbreviations follow Compagno (2001). Numbers in parentheses are those used for measurements by Yano & Musick (1992). * denotes proportional measurements for QM I.34963 which fall outside the range in Yano & Musick (1992).

| TL (mm) 2770 | | | | | |
|---|---|---|---|---|---|
| Measurement | Proportional dimension (%TL) | Yano & Musick (1992) range (%TL) | Measurement | Proportional dimension (%TL) | Yano & Musick (1992) range (%TL) |
| PRN (1) | 4.15 | 2.61-4.79 | D1B (32) | 26.71 | 15.45-36.34 |
| POB (2) | 5.31 | 3.73-7.31 | D1P (33) | 11.37 | 4.89-14.64 |
| PSP (3) | 8.56 | 7.39-12.16 | D1H (34) | 5.23* | 2.25-3.91 |
| POR (4) | 4.58 | 2.72-6.53 | D1A | 14.44 | - |
| PG1 (5) | 14.80 | 12.02-19.02 | D1I | 1.44 | - |
| PG2 | 16.34 | - | D2L (35) | 15.16 | 11.88-16.49 |
| PG3 (6) | 17.36 | 14.86-21.68 | D2B (36) | 12.20 | 9.96-15.05 |
| PG4 | 18.33 | - | D2P (37) | 8.12 | 4.31-8.81 |
| PG5 (7) | 19.15 | 16.13-23.52 | D2H (38) | 7.29 | 4.48-7.65 |
| PP1 (8) | 18.95 | 16.00-23.11 | D2A | 13.54 | - |
| PP2 (9) | 56.25 | 50.69-56.44 | D2I | 2.96 | - |
| SVL (10) | 59.21 | 54.66-60.93 | ANL (39) | 11.37* | 8.59-11.04 |
| PD1 (11) | 29.60 | 28.38-38.18 | ANB (40) | 10.29* | 7.02-9.82 |
| PD2 (12) | 64.26 | 60.53-67.43 | ANP (41) | 4.77 | 3.45-6.95 |
| PAL (13) | 68.59 | 63.39-74.18 | ANH (42) | 4.84 | 2.59-5.38 |
| PCL dorsal (14) | 80.79 | 77.33-83.32 | ANA | 9.68 | - |
| PCL ventral (15) | 80.25 | 74.44-81.61 | ANI | 1.08 | - |
| IDS (16) | 9.46 | 6.34-13.79 | P1L | 11.19 | - |
| DCS (17) | 3.25 | 2.46-5.62 | P1B (43) | 5.16 | 4.11-11.38 |
| PPS (18) | 33.21 | 26.35-35.13 | P1H | 9.78 | - |
| PAS (19) | 6.75 | 4.28-10.50 | P1A (44) | 11.73* | 4.96-11.11 |
| ACS (20) | 2.89 | 1.35-4.66 | P1I (45) | 4.26 | 3.33-5.45 |
| VCL | 19.31 | - | P1P (46) | 11.88* | 4.73-8.43 |
| PCA | 7.04 | - | P2L (47) | 9.93 | 7.99-10.91 |
| PPO (21) | 37.94 | 29.65-40.14 | P2B (48) | 8.09* | 5.25-8.00 |
| INW (22) | 4.22 | 3.76-5.32 | P2H | 5.56 | - |
| NOW | 1.48 | - | P2A (49) | 8.16 | 4.99-9.33 |
| ANF | 0.47 | - | P2I | 2.31 | - |
| MOW (23) | 10.29 | 7.49-13.09 | P2P | 5.31 | - |
| ULA | 0.47 | - | CL1 (50) | 9.10 | 3.74-9.20 |
| LLA | 0.79 | - | CLO | 5.31 | - |
| ING | 4.30 | - | CLB | 1.48 | - |
| GS1 (24) | 2.31 | 1.69-2.69 | CPH | 4.55 | - |
| GS2 | 2.56 | - | CPW | 2.35 | - |
| GS3 (25) | 3.03* | 2.03-2.88 | CDM (51) | 19.31 | 17.45-21.80 |
| GS4 | 2.92 | - | CPV (52) | 8.48 | 7.33-9.82 |
| GS5 (26) | 2.17 | 1.35-2.59 | CPU | 13.72 | - |
| ESL | 1.55 | - | CTR (53) | 4.95 | 3.33-5.32 |
| SPL (27) | 1.34 | 0.78-2.30 | CST (54) | 3.39* | 1.82-3.26 |
| EYL (28) | 2.67 | 2.26-4.09 | CTL | 5.20 | - |
| EYH (29) | 1.52 | 0.64-1.83 | TRW (55) | 13.36 | 9.14-16.86 |
| INO (30) | 4.62* | 5.49-10.02 | TRH (56) | 11.91 | 5.77-14.18 |
| DIL (31) | 28.16 | 17.31-37.66 | | | |

FIG. 2. *Pseudotriakis microdon* Tanjung Luar fish landing site, Lombok. (Photo: Fahmi).

islands of Dana, Raijua and Sawu in the Sawu Sea, midway between Sumba and West Timor (~11°00' S, 121°30-40' E) in depths between 100 and 150m. Demersal longlines (one per boat, ~1,000m in length, with ~100 large hooks on 3m traces) are employed. The shark was processed by the fishers on site, for its meat, fins, skin and possibly the liver. Only total length and sex of the individual were recorded, and although no detailed examination of the dissection was carried out, the individual possessed mature female reproductive organs but was not gravid. The catch from this fishing boat also included two medium-sized *H. griseus* and at least one large *Carcharhinus obscurus* (Lesueur, 1818).

## DISCUSSION

The new Australian and Indonesian records were easily identified as *P. microdon* from the descriptions and characters given in Compagno (1984, 1988). Consistent with the separation of *Pseudotriakis* from *Gollum*, the first dorsal fin height (D1H) was considerably lower than the second dorsal fin height (D2H) (QM I.34963; D1H 0.7 in D2H). The majority of measurements on the Australian specimen fall within the range of those presented in Yano & Musick (1992) and those that do not are generally close to the range presented (see Table 1). The exceptions are D1H and P1P (pectoral fin posterior margin). These differences are likely due to slight differences in measuring techniques between the methods followed here (Compagno, 2001) and those used by Yano & Musick (1992), or from general variability. Indeed, Gilhen & Coad (1999) report a D1H of 4.5%TL for a Canadian specimen, also outside the range given by Yano & Musick (1992). From the data presented in Table 1 it is clear that there is considerable variability in some morphometric characters in this species (Taniuchi et al., 1984; Yano & Musick, 1992). This is to be expected in deepwater chondrichthyans with flabby, easily deformed bodies. Baranes (2003) reported that a Seychelles specimen possessed a crest in continuation of the anterior margin of the first dorsal fin and that his morphometrics varied from those in the literature. However, most of his proportional measurements fall within or just outside the range presented in Yano & Musick (1992) (to which Baranes (2003) did not compare his specimen). The exception is pre-first dorsal fin (PD1) which is considerably lower due to the presence of the pre-dorsal crest, the origin of which Baranes (2003) took to be the origin of the first dorsal fin. The first dorsal-fin origin is difficult to assess in *Pseudotriakis* and this may lead to reported variation. Although PD1 is lower in the Seychelles specimen, first dorsal fin base (D1B) is within the reported range.

The maximum observed size of *P. microdon* is 296cm and 295cm TL for females and males, respectively (Yano, 1992). Variation in size at maturity is apparent from the literature. Compagno (1984) specified mature males as

small as 200cm TL. Yano (1992), based on a 250cm TL immature male and nine mature males greater than 261cm TL, concluded maturity in males is reached at ~260cm TL; whereas, Gilhen & Coad (1999) and Taniuchi et al. (1984) reported smaller adult males, of 223 and 228cm TL, respectively. The Australian specimen had completely calcified claspers, and at 277cm TL, is in the documented range of mature males. Forster et al. (1970) erroneously reported Saemundsson's (1922) gravid female at 212cm TL, while it was Saemundsson's male specimen that was this size and the gravid female was in fact reported in Saemundsson (1922) as "9 foot" (274cm TL). Reliable reports of female maturity in the literature start at 256cm TL (Forster et al., 1970) and the Indonesian female reported here at 287cm TL was mature. Documented size at birth is also variable, with Compagno (1984) suggesting 70-85cm TL, Saemundsson (1922) reporting near term embryos of 85cm TL from Icelandic waters, and Taniuchi et al. (1984) reporting a 96cm free-swimming individual (no details were provided). However, these are considerably lower than other reports of near-term embryos, i.e. 112 and 113cm TL (Sea of Kumanonada, Honshu, Japan; Taniuchi et al., 1984), 116-120cm TL (Okinawa Islands, Japan; Yano, 1992) and 138cm TL (Challenger Plateau, New Zealand; Stewart, 2000). Yano (1992) reported that a 156cm TL female possessed an umbilical scar which was 22mm long and 6mm wide. Stewart & Clark (1988) did not comment on the presence or absence of an umbilical scar in a 155.5cm TL male. Given its rarity, very little is known of the biology of *P. microdon*. Yano (1992) reviewed reproductive biology, confirming Forster et al.'s (1970) suggestion that the species was oophagous. Saemundsson (1922), Taniuchi et al. (1984), Yano (1992) and Stewart (2000) report litter sizes of two, while the gestation period is unknown (but is presumed to be extended).

Only a single *P. microdon* has been recorded in southeastern Indonesia during a comprehensive survey of a number of fish landing sites in this region between April 2001 and October 2004, in which time a total of ~36,000 individual chondrichthyans, representing ~138 species, were recorded. However, it should be noted that deepwater fisheries in Indonesia are very limited and only little demersal fishing occurs in depths >300m and none in depths >600m. Also, only small-scale longlining occurs in these deeper waters, i.e. there is no trawling. If fisheries in Indonesia did begin to operate in deeper waters, larger numbers of *P. microdon* may be encountered along with other slope species. At the Tanjung Luar landing site in Lombok, the local name used for *P. microdon* was "hiu tahu" (Bahasa Indonesia). It is not known whether this name applies solely to *P. microdon* (which would indicate that individuals may be caught on an irregular basis by fishers at this site, and perhaps elsewhere in Indonesia) or if it is used for a number of deeper water species.

The first Australian record, a 200cm TL female (WAM P.30826-001) was captured by a trawler targeting orange roughy (*Hoplostethus atlanticus*) off Cape Leeuwin (~35°00′S, 114°45′E), Western Australia at 830m depth on 10/08/1994 (Allen & Cowan, 1995). Other Southern Hemisphere records are presently confined to those from Aldabra and Cosmoledo Islands (to the north of Madagascar) and Geyser Reef (between Madagascar and the Comoros) in the western Indian Ocean (Forster et al., 1970) and from around New Zealand, where numerous specimens have been reported. The species has been recorded from three isolated locations around the North Island of New Zealand: Challenger Plateau to the west (Stewart, 2000); Hikurangi Trough off the eastern coast (Stewart & Clark, 1988; Stewart, 2000); and, Three Kings Ridge to the north (Yano, 1992). Given these records, it is highly likely that the species has a much wider distribution than presently known around New Zealand. The same can be implied for other regions, and as global deepwater fishing activities continue to expand and as further deepwater areas and environments are surveyed, the known distribution of *P. microdon* will likely be widened. Such catches and records will require close monitoring, not only to better define the species' distribution, but to ensure that such a rare, large, and reproductively limited chondrichthyan, does not suffer population collapse or localised extirpation (Cavanagh et al., 2003).

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# THE TRAPDOOR SPIDER *ARBANITIS* L. KOCH (IDIOPIDAE: MYGALOMORPHAE) IN AUSTRALIA

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The type species of *Arbanitis* L. Koch, 1874, *A. longipes* (L. Koch, 1873) is redescribed from the rediscovered holotype male; from new conspecific material, males and females are diagnosed, and their distribution, habitat, and burrow are described. Several somatically diagnosable populations from southeastern Queensland and northern New South Wales are also identified and their variation described. *A. longipes* fits the previous diagnosis of *Misgolas* Karsch, 1878. A cladistic analysis of some *Misgolas*, *Euoplos*, *Cataxia* and *Homogona* species and the new species described herein provides support for the continued maintenance of *Misgolas* along with its rediagnosis. *Arbanitis* is radically rediagnosed and now includes only the type species and two new species from the Macpherson Ranges (*A. robertcollinsi*) and northern New South Wales (*A. beaury*). Three new *Misgolas* species—*M. bithongabel*, from Lamington Plateau and two others, closely allopatric or sympatric (*M. echo*, *M. monteithi*), are also described. *Arbanitis*, as here defined, is the plesiomorphic sister group of other Australian idiopids; biogeographic derivation from that indicates that the *A. longipes* species-group arose on the Lamington Plateau (above 600m) and the lowland species (*A. longipes*) survives in habitats from rainforest to remnant open forest.

A key to Australian idiopid genera is provided. The process of matching conspecific males and females of sympatric congeners in somatically homogenous groups is discussed. Of the five new species, females of *Arbanitis robertcollinsi* and *Misgolas* species cannot be described because they are not confidently diagnosable; intervention of molecular methods to match them with conspecific males is proposed. *Misgolas pulchra* (Rainbow & Pulleine, 1918) is synonymised with *Arbanitis longipes*. Species previously included in *Arbanitis* (except *A. longipes*) are transferred to the resurrected *Euoplos* Rainbow, 1914; all New Zealand species are removed from the synonymy of *Arbanitis* and restored to *Cantuaria* Hogg. □ *Mygalomorphae, Idiopidae, Australia, biodiversity, rainforest.*

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Unlike most spiders commonly surveyed, the Mygalomorphae are long-lived and often subterranean. Mating maximally once each year and highly sedentary, they are ideal animals for surveys of soil and forest integrity, and especially effective for short-term surveys. Mygalomorphs, at least in northern and eastern Australia, are taxonomically better known than their araneomorph sisters. The exceptions are the ubiquitous Idiopidae.

Idiopids occur through most parts of Australia, notably absent from the far north and from Pacific islands including New Caledonia, but present in New Zealand and Tasmania (Raven, 1985). They have exploited the most diverse habitats—desert, open forest, rainforest, montane areas snow-covered in winter, mangrove and other nearby maritime habitats (Main, 1981; Churchill & Raven, 1992).

Among idiopids of eastern Australia is a group of spiders which are quite attractive and distinctive. The yellow brown carapace with a strongly arched caput contrasts with the stout yellow- to red-brown legs. The spiders build burrows in embankments with a thick plug door often encrusted with moss. These spiders have been placed in *Arbanitis* L. Koch, 1874 (e.g., Main, 1985a, b). A second idiopid, *Misgolas* Karsch, 1878, is the subject of ongoing studies (Wishart, 1992) but differs from species placed in *Arbanitis* by Main (1985a) in the relatively lighter build and slender brown hirsute carapace; many species have dark brown stripes or decorations on the retrolateral face of the pedal

FIG. 1. *Arbanitis longipes* (L. Koch, 1873): A, B, F, female habitus, dorsal (A), lateral (B), ventral legs showing decorations (F). C, D, burrow entrance in open forest Camira (C, E), D, embankment beside rainforest, "End of the World", Pine Mountain.

femora, patellae and tibiae and palp. One of us (GW) is revising *Misgolas* Karsch, 1878 and is finding a very diverse, new fauna. At present, the Australian complement of *Misgolas* numbers 19 species; the real complement is predicted to be about 6 times that (as Raven, 1988, had predicted would be the average difference between known and new species for all Australian spiders). So *Misgolas* is highly speciose.

L. Koch (1873) described *Pholeuon longipes*, from a single male from Bowen, northeastern Queensland. However, the generic name was

pre-occupied and was replaced by *Arbanitis* L. Koch, 1874. The genus remained monotypic until Hogg (1903) described *A. maculipes*, later synonymised with *A. annulipes* (C. L. Koch, 1841). Rainbow & Pulleine (1918) included seven species in *Arbanitis*. Of those, only two were retained by Main (1985a, b). In Main's studies on Australian idiopids (e.g. Main, 1985a, 1967), a concept of *Arbanitis* was formed in the absence of firsthand knowledge of the type species. The type specimen was considered lost (Main, 1985a, b). Despite this, her synonymy (Main, 1985a) of *Arbanitis* included eight other valid names (including two New Zealand genera) and was probably the largest generic synonymy in Australian spiders.

Unusual amongst Australian idiopids, the male of *A. longipes* lacks a tibial spur. Raven (1985) concluded that a tibial spur is plesiomorphic in the Idiopidae; hence, the absence of a spur in *A. longipes* must be considered a secondary loss. One of us (RJR) checked all collections in Australian museums for spur-less males assignable to *Arbanitis* (sensu Main) from northern Queensland (from Bowen, north). None were found but the sampling in the Bowen region could not be considered long term or intensive. Main (1985a) reported a similar failure to locate new material of *A. longipes*.

In June, 1998, RJR visited the Zoologisches Universitat und Zoologisches Museum, Hamburg, to examine problematical araneomorph taxa. The former curator, Dr Gisela Rack, had specific material set aside for examination. This was from the Godeffroy collection on which Ludwig Koch's pivotal publication, *Die Arachniden Australiens*, was based. The handwriting on the labels of that material had faded but the Godeffroy badge was still distinct. A number of specimens with such labels were examined but only two were then recognised: the holotype males (previously presumed lost) of *A. longipes* (L. Koch, 1873) and of *Habronestes spirafer* L. Koch, 1873. The latter will be dealt with elsewhere. In both cases, the definitive characters of the male from Koch's figures and descriptions were clear and faithfully illustrated.

The re-discovery of the holotype of *Arbanitis longipes* was met with considerable unease when it was noted that it bore very strong resemblance to species currently included in *Misgolas* and differed substantially from Main's (1985a) concept of *Arbanitis*. Hence, species (other than the type) previously included in *Arbanitis* by Main (1985a) required a separate generic name; the oldest available name for those species is *Euoplos* Rainbow, 1914.

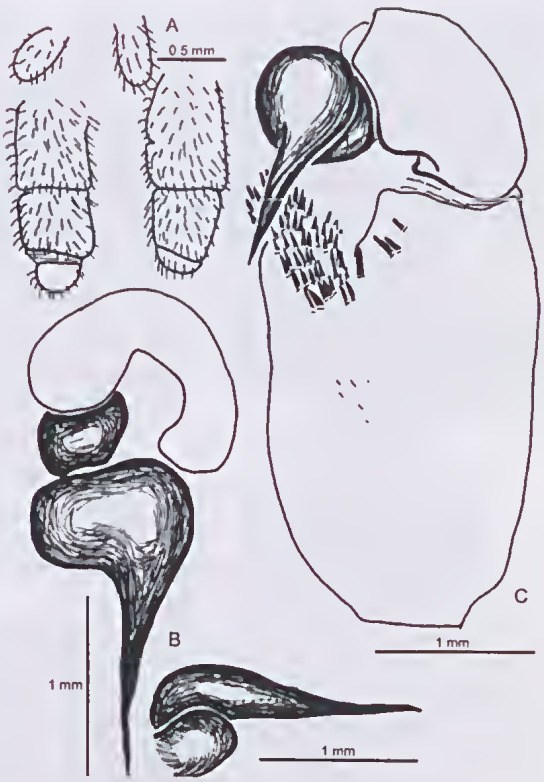


FIG. 2. *Arbanitis longipes* (L. Koch, 1873), holotype male: A, spinnerets, ventral view; B, palpal bulb, ventral and retrolateral view; C, palpal tibia, tarsus and bulb, retrolateral view.

The problem of difficult-to-recognise type species was not, however, confined to *Arbanitis*. The type species of *Misgolas*, *M. rapax* Karsch, 1878, has a badly damaged, dried female as holotype from New South Wales. As seen below, the problems of identifying females of closely related *Misgolas* are substantial and only compounded by the vague type locality and damaged holotype. Despite substantial knowledge of *Misgolas* from New South Wales, GW could only conclude that *M. rapax* is a species incertae sedis. However, GW was able to use some leg muscle of the holotype to extract DNA and match it against fresh specimens and males and establish the species identity of *M. rapax*.

The questions addressed here are whether *Misgolas* and the newly defined *Arbanitis* are congeneric, to which genus are the New Zealand species of *Misgolas* related, and what are the relationships of the groups. The potential effect of the change of names widened when Raven (1985) transferred all (New Zealand) species of *Cantuaria* Hogg, 1902 to *Misgolas*. We review the New Zealand Idiopidae elsewhere.

## MATERIALS AND METHODS

Abbreviations are standard for the Mygalomorphae and are given in Raven (1994). Institutional acronyms are given with the acknowledgements.

## SYSTEMATICS

### Family IDIOPIDAE
### Subfamily ARBANITINAE

### KEY TO GENERA OF THE AUSTRALIAN ARBANITINAE

1. Fovea deeply procurved or U-shaped . . . . *Euoplos*, part
   Fovea not as above . . . . . 2
2. Cuspules (female) or spinules (male) present on labium . 3
   Neither cuspules nor spinules present in either sex . . . 5
3. Cuspules extend for length of maxillae . . . . *Homogona*
   Cuspules confined to inner edge of maxillae . . . . . 4
4. Rastellum of 3-4 large conical spines on distinct mound . . . . . *Blakistonia*, part
   Rastellum weak and not on mound, if present . . *Cataxia*
5. Eye group clearly wider in back . . . . . 6
   Eye group distinctly wider in front than behind or parallel-sided . . . . . 10
6. Dorsal abdominal sigilla present . . . . . 7
   Dorsal abdominal sigilla absent . . . . . 8
7. Dorsal abdomen with coriaceous corrugations . *Idiosoma*
   Dorsal abdomen not as above . . . . . *Aganippe*
8. Eye group roughly rectangular . . . . . *Euoplos*, part
   Eye group strongly trapezoidal, much wider behind than in front. . . . . 9
9. Carapace much longer than wide; caput low . . . *Anidiops*
   Carapace little longer than wide; caput steeply arched . . . . . *Eucyrtops*
10. Eye group about as long as wide . . . . *Blakistonia*, part
    Eye group clearly wider than long. . . . . 11
11. Carapace broad, females with strongly procurved fovea . . . . . *Euoplos*, part
    Carapace narrow (Fig. 3A), females with straight fovea . . . . . 12
12. Males with long spines on palpal tibial apophysis . . . . . *Arbanitis*
    Males with short conical spines on palpal tibial apophysis . . . . . *Misgolas*

REMARKS. Subfamily diagnosis and distribution as in Raven (1985).

### Arbanitis L. Koch, 1874

*Pholeuon* L. Koch, 1873: 471. Type species by monotypy *Pholeuon longipes* L. Koch, 1873 preoccupied by *Pholeuon* Hampe, 1856.
*Arbanitis* L. Koch, 1874: 491, replacement name for *Pholeuon* L. Koch, 1873.

DIAGNOSIS. Differs from *Cantuaria* in having plesiomorphic wide posterior book-lung apertures and from *Misgolas* and *Euoplos* in the rounded cymbial lobe, simple unadorned spiniform embolus, the long spines on the RTA and further from *Misgolas* in the absence both of a spur on tibia 1 and of a distal process on the retrolateral palpal tibia in males.

Species here attributed to *Arbanitis* are consistent in the subquadrate eye group shape which is narrower behind than in front; tarsi I, II of males never incrassate ventrally (as in *Euoplos*); labium always wider than long. No spines, spinules or cuspules on the labium.

TYPE SPECIES. *Pholeuon longipes* L. Koch, 1873 by monotypy.

REMARKS. All *Arbanitis* have a very uniform eye configuration: the eye group is clearly wider in front than behind, the PLE arc clearly smaller than AME or ALE, the PME are tiny. That is also the case in some species of *Misgolas*. Using this diagnosis, it is not yet possible to distinguish females of *Arbanitis* from those of *Misgolas*.

DISTRIBUTION & HABITAT. *Arbanitis* is known only from southeastern Queensland, including the Lamington Plateau and just southwest of that area in northern New South Wales. Most localities are rainforest, wet sclerophyll or heath with some populations in open forest.

SPECIES INCLUDED. *Arbanitis longipes* (L. Koch, 1873), *Arbanitis robertcollinsi*, sp. nov., *Arbanitis beaury*, sp. nov.

### Arbanitis longipes (L. Koch, 1873)
### (Figs 1-4, 5A-D, 12, 13A)

*Pholeuon longipes* L. Koch, 1873: 472.
*Arbanitis longipes* L. Koch, 1874: 491; Hogg, 1901: 236, f. 24c; Rainbow, 1914: 213, f. 26-27; Main, 1985b: 18.
*Arbanitis pulchellus* Rainbow & Pulleine, 1918: 114 (presumed replacement name for *Arbanitis pulchra* Rainbow & Pulleine, 1918: 86, *nomen nudum*). NEW SYNONYMY.
*Aname pulchra* Rainbow & Pulleine, 1918: 153. First synonymised with *Arbanitis pulchellus* Rainbow & Pulleine, 1918 by Main, 1972: 100.
*Misgolas pulchellus*: Main, 1985b: 24.

TYPES. Holotype ♂, putatively "Bowen" here corrected to Camira, Brisbane (*Arbanitis longipes*), ZMH; holotype

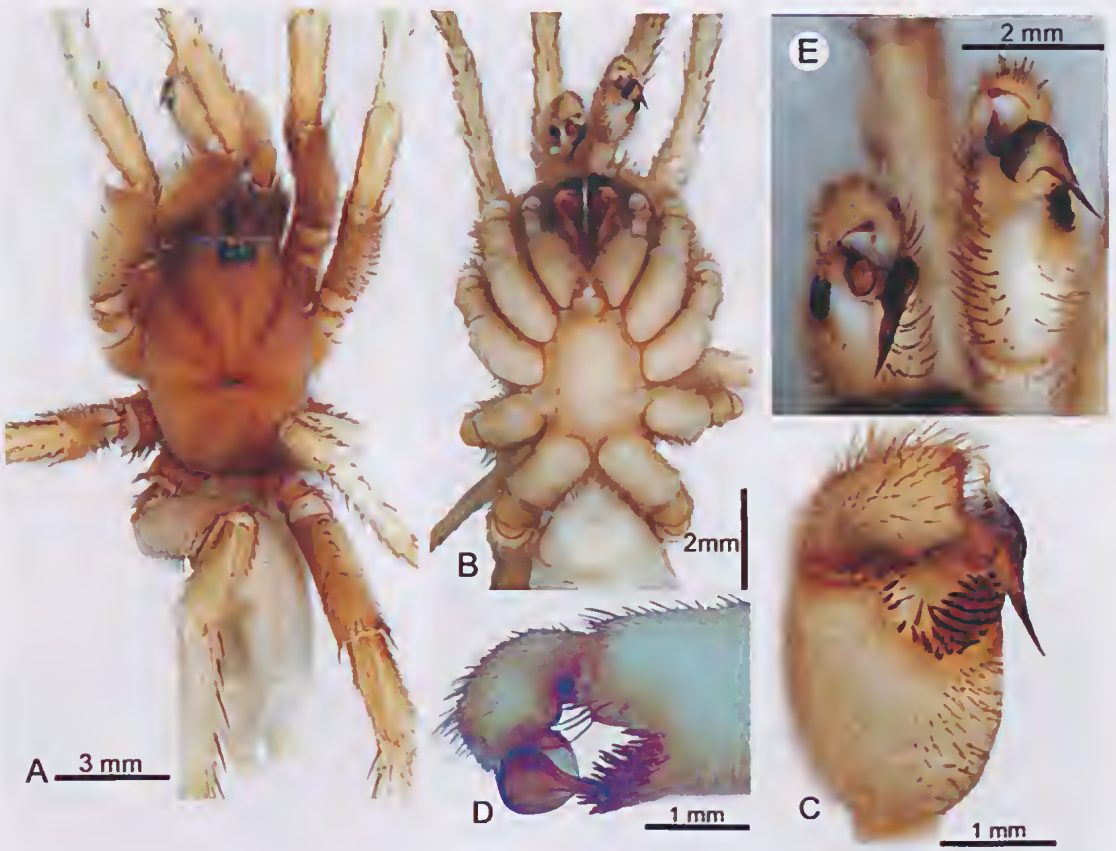


FIG. 3. *Arbanitis longipes* (L. Koch, 1873), holotype male: A, caparace and abdomen, dorsal view ; B, sternum, coxae and mouthparts, ventral view; C-E, palp and bulb, ventral (E), retrolateral distal showing lines of spines (D), and retrolateral view showing rounded cymbial lobe and RTA (C).

♂, Mt Tamborine, AM K40993, KS8375 (*Aname pulchra*), examined.

MATERIAL EXAMINED. QM S19519, 1 ♂, Beerwah Forestry Reserve, 26°51'S 152°57'E, M. Glover; QM S8909, 9041, 2 ♂♂, Bahrs Scrub, 27°45'S 153°10'E, rainforest, pitfall, 30 Apr 1980-29 Jan 1981, G & S. Monteith; QM S25921, 1 ♂, Camira, 27°37'S 152°55'E, 5 Nov 1994, A. Patterson; QM S20632, 2 ♂♂, Glen Witheren Main Scrub, 28°03'S 153°10'E, rainforest, pitfall and intercept traps, 3 Oct-31 Dec 1991, G. Monteith; QM S22410, S22412, 4 ♀♀, Enoggera, Army Lands, 27°26'S 152°58'E, 6 Jan 1994, T. B. Churchill; QM S54311, 54313, 2 ♂♂, The Knobby, 4km west of Glamorgan Vale, 27°30'S 152°35'E, semi-evergreen vine thicket, pitfall, 13 Jan-16 May 1999, G. Monteith; QM S6709, ♀, Mt Cotton, nr Venmans Reserve, 27°37'S 153°13'E, Feb 1987, M. Maher; QM S8994, female, Capalaba, Leslie-Harrison Dam, 27°31'S 153°11'E, 8 Nov 1976, R. Hiatt; QM S9080,1 ♂, Teviot Falls, via Boonah, 28°13'S 152°28'E, rainforest, pitfall, 25 Aug-3 Oct 1976, G & S. Monteith. Brookfield, Gold Ck Reservoir, 27°29'S 152°55'E, rainforest: QM S8971, 1 ♀, 25 Aug 1979, R.J. Raven; QM S20625, 2 juveniles, night collection, 22 Jan 1981, V. Davies, R. Raven; QM S20626, 1 ♀, 30 Oct 1980, V. Davies, R. Raven. Pine Mt, Ipswich, 27°30'S 152°44'E, rainforest, pitfall: QM S9068, 1 ♂, 20 May-11 Aug 1976, G & S. Monteith; QM S9072, ♂, 27 Feb-20 May 1976, G & S. Monteith; QM S57951, 1 ♂, Pine Mountain Environmental Park, 27°32'S 152°42'E, open forest, pitfall, 11 Nov 1998-13 Jan 1999, G. Monteith, D. Cook, G. Thompson. QM S9793, 1 ♀, Toowong, 27°28'S 153°00'E, 7 Jan 1989, A. Fay; Rochedale State Forest, 27°37'S 153°08'E, open forest: QM S8968, ♀ litter, 20 Sep 1979, R. Raven, V. Davies; QM S8969, 1 ♀, 21 Aug 1980, R.J. Raven; QM S8977, ♀, 20 Sep 1979, R. Raven, V. Davies; QM S20628, ♂, pitfall, 7 Jul 1979, R. Raven, V. Davies; QM S9104, ♀, 5 Apr 1973, R.J. Raven; QM S20614, 1 ♀, 1 juvenile, 20 Dec 1979, V. Davies, R. Raven; QM S20615, 1 ♀ 12 Jun 1980, V. Davies, R. Raven; QM S20619, 2 juveniles, in burrows, 20 Jul 1979, R. Raven, V. Davies; QM S20620, 31 Jan 1980, R.J. Raven; QM S20624, 3 ♀♀, 1 Jul 1980, R. Raven. Camerons Scrub, 27°29-30'S 152°43-44'E, vine scrub, pitfall: QM S49703, 49707, 3 ♂♂, 11 Nov 1998-13 Jan 1999, G. Monteith, G. Thompson, D. Cook; QM S54308-10, S54312, 4 ♂♂, 13

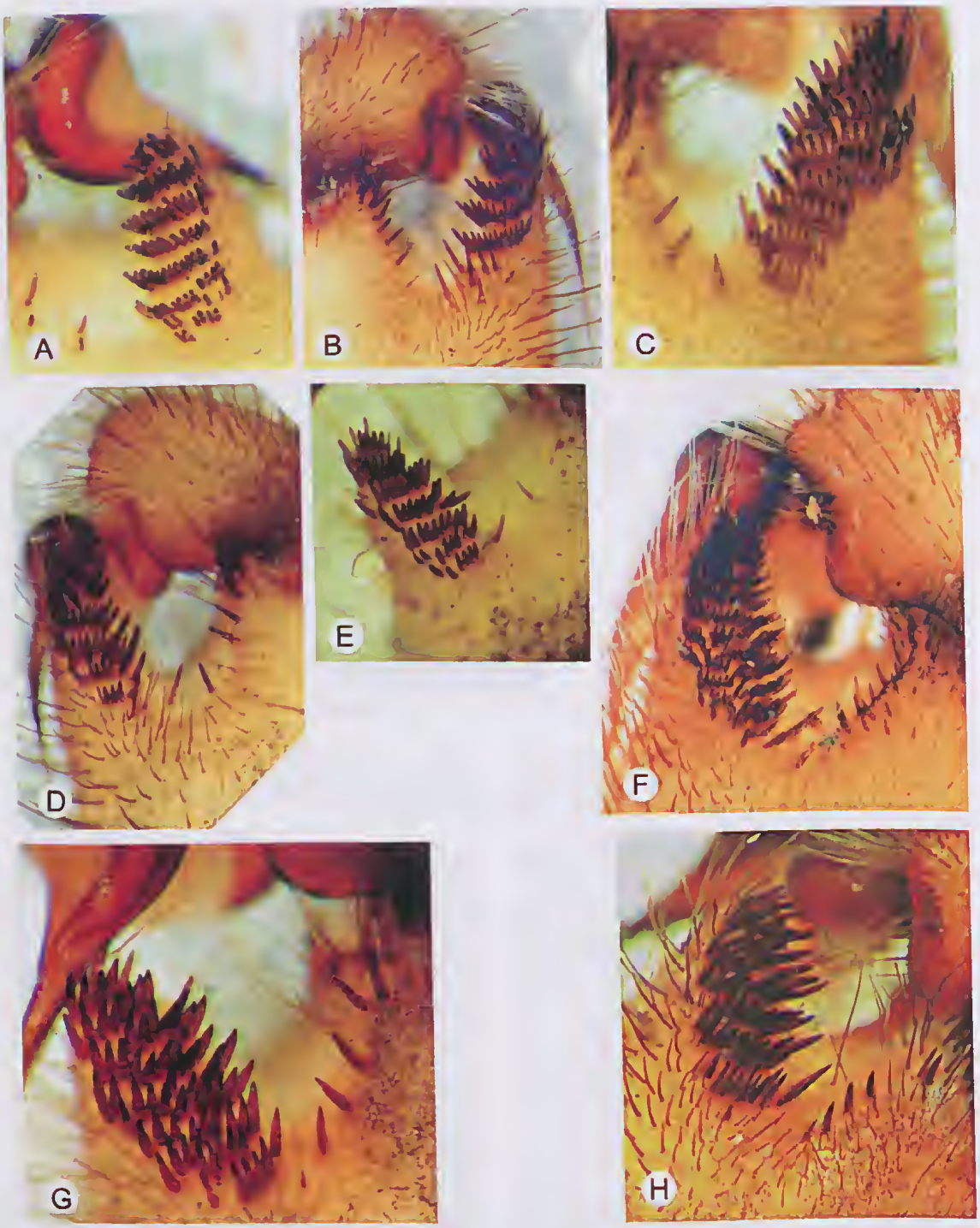


FIG. 4. *Arbanitis longipes* (L. Koch, 1873), retrolateral view of RTA of males showing variation in spines per row and number of rows: A, Rosens Lookout, Beechmont, QM S9124; B. Bahrs Scrub, QM S8909; C, Flinton Hill, qm S9072; D, Beerwah, QM; E, Teviot Falls, QM S9080; F, Mt Tamborine, QM S54307; G, Rochedale State Forest QM S20628; H, Camira, QM S25921

Jan-6 May 1999, G. Monteith. Mt Tamborine, 27°55'S 153°11'E, rainforest: QM S54307, ♀, pitfall, Nov 1978-14 Jan 1979; QM S54324, 1 ♀, V. Salanitri; QM S9012, 2 ♀♀, 23 Oct 1912, Hacker; QM S8980, 4 ♂♂, Dalby Property, Summer 1980/81, P. Ogilvie; QM S8970, ♂, 19 Oct 1980, J. Mariott; QM S9135, ♀, Palm Grove, pitfall, 25 May-13 Oct 1975, G. & S. Monteith. Rozens Lookout, Beechmont, 28°07'S 153°11'E, rainforest, pitfall, G. & S. Monteith: QM S9123, ♂, 25 May-30 Aug 1975; QM S9124, male, 26 Oct-14 Dec 1974. SAM NN2869-70 (1992654-5), ♀ & juvenile, Kedron Brook, Brisbane, [27°25'S, 153°02'E], 1912, R.H. Pulleine, labelled as "*Arbanitis pulchra*, R.". All in SE.Q.

DIAGNOSIS. Males differ from those of *A. robertcollinsi* sp. nov. and *A. beaury*, sp. nov. in having RTA spines in 4-9 ordered ranks, and further from *A. beaury*, sp. nov. in having only bristles on the cymbium. Females have basifemoral thorns only on IV. Males and females with dark bar on prolateral and retrolateral face of femora, patellae, and tibiae I-IV.

DESCRIPTION. HOLOTYPE ♂. Carapace 6.06 long, 4.18 wide. Abdomen 6.68 long, 3.43 wide. Total length, 15.

*Colour in alcohol*. Carapace orange brown with darker striae, eyes with black edges but entire region not dark; chelicerae red brown. Abdomen presumably faded, fawn coloured. Legs yellow brown, prolaterally and retrolaterally patellae, tibiae and to lesser extent metatarsi I, II with darker faces.

*Carapace*. Bands of long silver hair on interstrial ridges and caput. Margins with band of 2-3 irregular lines of short black thick curved bristles forming roughly triangular area posteriorly. Few dark (weak) bristles on interstrial ridges. Fovea wide, straight with recurved edges. Large recurved bristle between AME, smaller curved one between PME. One long and two short weak anteromedial bristles.

*Eyes*. Eight in two rows, front row strongly procurved and clearly wider than slightly recurved back row. Set on low mound extending forward to include clypeus. Group front width: back width: length, 42: 36: 25; anterior ocular quadrangle front width: back width: length, 42: 21: 18. AME: ALE: PME: PLE, 10: 14: 6: 7. Interspaces as AME diameter: AME-AME, 0.4; AME-ALE, 0.5.

*Chelicerae*. Long, slender with hirsute triangular band entally. Bristles become thicker and shorter towards fang. Rastellum strong: irregular line of 7 short thick spines from inner edge about half of fang edge with 2-3 spines behind that. Intercheliceral tumescence a moderately large pallid area. Fangs long without outer keels or ridges, no serrations on ventral keel. Furrow promargin with 6 small spaced teeth, retrobasally a line of 5 smaller teeth.

*Maxillae*. Long, with rounded heel with *ca*. 9 laneeolate cuspules on anterior inner edge. Anterior lobe distinct but without defining groove.

*Labium*. *ca*. twice as wide as long, without cuspules or spinules; anteriorly indented with median transverse mound; bristle clusters on lateral lobes anteriorly. Labiosternal groove a continuous wide groove, ending just before sternum edge.

*Sternum*. Narrow, widest at coxa II. Bristles slightly thicker on submargins than centrally; uniform cover of long bristles, fine hairs and short setae. Sigilla: anterior and middle small, within 0.5 diameter of margin, posterior similar size but 1 diameter remote from edge.

*Legs*. Coxae without strong setal clusters; inner edges rounded. Generally covered with strong bristles and spines. Tibia 1 without modified enlarged spines or spurs. Metatarsi and tarsi I, and tarsi II gently dorsoventrally bowed, metatarsi 1 laterally flattened distally. All legs long, slender.

*Scopula*. Scopulate areas of I, II pallid, without setae or spines. Long hairs, moderately dense, and extending to lateral edges for distal half of metatarsi I, II; scattered hairs only on III. Dense, full, entire but short on tarsi I, II, sparse and intermixed with spines and bristles on III, no scopuliform hairs on IV.

*Trichobothria*. Cymbium medially with 2 lines of 4-5 filiform trichobothria separated by setae. Metatarsi with long line becoming irregular distally. Tarsi with irregular narrow band (=narrow zigzag) for length.

*Spines*. Spines in line along edges or in cluster are represented as p4, if paired they are shown as 2.1.1. I: fe p2d5; pa p2v2; ti p3v5.1.4.3; me p1v1.1.2; ta 0. II: fe p2d4; pa p3; ti p2v3.1.3.1.3; me p2v1.2.1.1; ta rv1. III: fe p1d3r2; pa p3; ti p3r2.1.1.1v2.2.1.3; me p4r2v2.1.2.2.1.3; ta p2pv5rv4. IV: fe d4r2; pa 0; ti r5 (long) v4.1.2.3; me p1r4v.1.2.1.2.1.1.3; ta pv6rv6. Palp: fe 0; pa p1; ti only on process; ta 0.

*Claws*. I: STC with long sinuous row from distally ental to basally mesal; all teeth of similar size but basal penultimate tooth longer; ITC slightly curved, bare. IV: short curved row of 5 similar teeth entally, clearly separated from basal pair of two larger teeth.

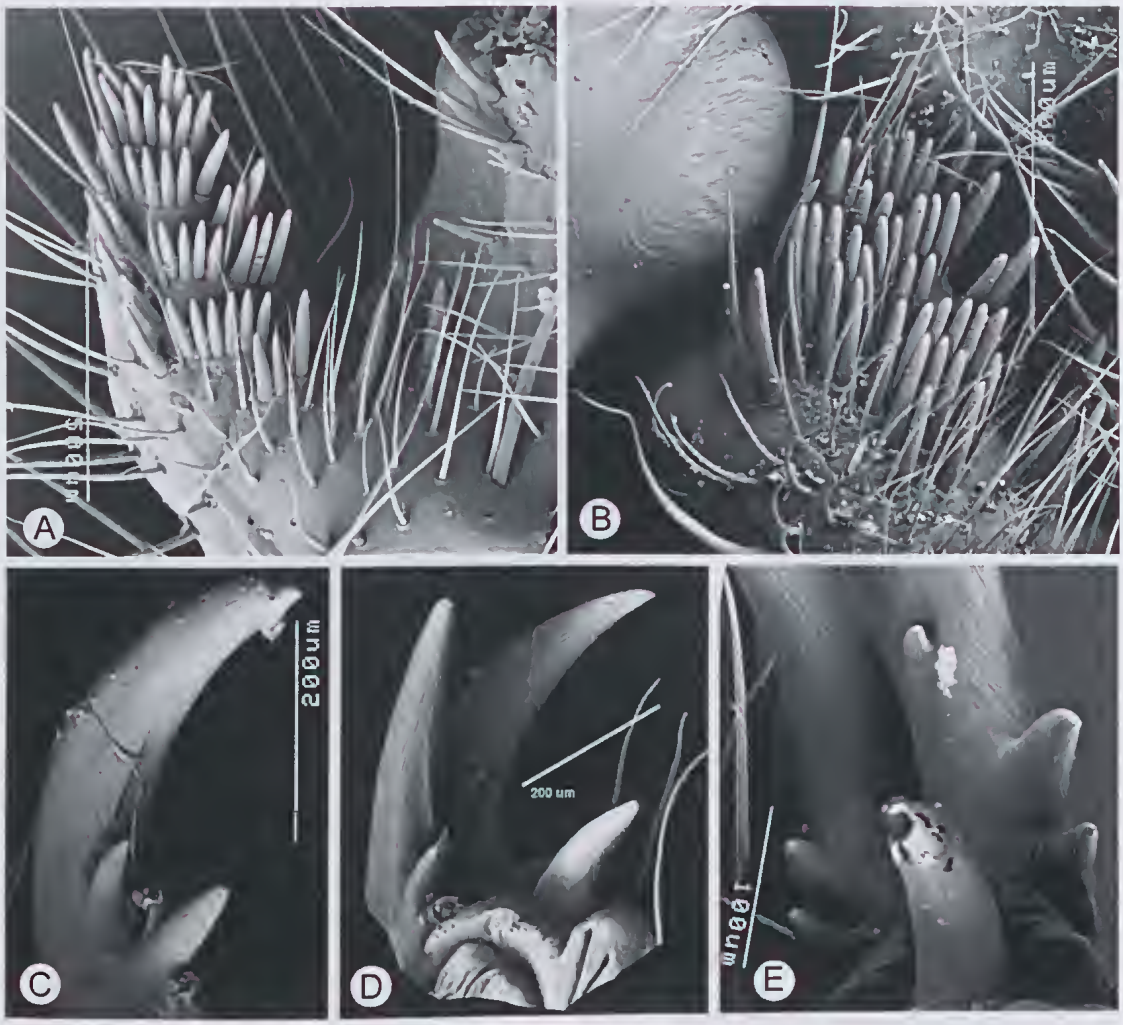


FIG. 5. *Arbanitis longipes* (L. Koch, 1873), scanning electron micrographs, A, C-E. A, RTA, Beerwah, retrolateral view; C, female palpal claw; claws on female leg I (D), and IV (E). B, *Arbanitis robertcollinsi*, sp. nov., RTA, retrolateral view.

*Palp*. Tibia slightly flattened laterally with strong distally directed retrolateral process in apical third; process extends beyond line off end of tibia; ventral half of tibia and inner edge of process pallid, unsclerotised; inner base of process abruptly joins tibia ventrally; setation on retrolateral tibia shorter than prolaterally. Process broad, conical with distinct transverse lines or rosettes of long spines retrolaterally, lineation disrupted apically by lines of 3, 7 and 3 apically; distal of process 6 long spines in short sloping area to end of tibia. Cymbium with short lobe forming angle of *ca*. 90° separated widely from short rounded prolateral lobe. Bulb: large basal subtegular lobe joined to tegulum by wide less sclerotised zone leading to continuous basal haematodocha; embolus tapers gradually to simple twisted tip.

*Spinnerets*. PMS large, distally lobular; PLS basal= middle> domed apical.

*Posterior Book-lungs*. Covers 1.37 wide, 1.12 long; aperture 0.67 wide, 0.10 deep, with fringe of long teeth across aperture.

♀ QM S8994. Carapace 7.63 long, 5.56 wide. Abdomen 8.88 long, 5.75 wide.

*Colour*. Carapace, chelicerae reddish-orange brown, carapace with narrow dark edge. Abdomen dorsally with dark solid broad brown

medial band breaking up in posterior third; 4 pairs of oval to tear-shaped fawn or unpigmented areas on ectal edge of medial band, anteriorly smallest area (by half) at 1/5, wide gap posteriorly to next and largest ovoid area, next two pairs larger, more tear-shaped and equidistant apart; narrow irregular band runs for length; after fourth pair of fawn ovoid patches brown weakens quickly to mottling almost to unpigmented just anterior to spines; two more pairs of ovoid fawn spots evident in posteriad; laterally, abdomen lightly mottled brown, ventrally entirely fawn, without brown mottling. Legs orange brown with dark "burnt" brown areas on pro- and retrolateral femora, patellae, tibiae of palp to leg II and metatarsi I, II; weaker such marks on femora III, IV, tibiae and metatarsi III, IV; reduced to distal collar and triangular shadow on patellae III, IV. Femora I, II also with longitudinal ovoid zone retrolaterally on I, II. Burnt zones extend for length of patellae, palpal tibiae, tibiae I, II and prolateral palpal patella but only distal half of retrolateral palpal patellae. Sternum, maxillae and labium red brown. Coxae I, II ventrally slightly brown in anterior half.

*Carapace*. Narrow, widest just anterior to fovea narrowing in gentle curve anteriorly and posteriorly. Striae deep, glabrous: anteriorly with wide deepening at mid-length, next is lenticular not reaching edge, next is short, oval just posterior to fovea, posterior pair long not reaching edge. Fovea broad, deep, straight to very slightly procurved, without enlarged setae. Pile of long white hair on interstrial ridges, thinner on margin. Lateral margins with short fine brown bristles. 3-4 weak bristles posterior of fovea and 2 thick on prefovea ridge in anterior half. *ca.* 10 brown bristles between PME, one long broken anterior to AME in AOQ; 2 large and 6 small on clypeus edge in front of eye group. ALE set 0.5 diameters from carapace edge.

*Eyes*. Occupy 0.28 of headwidth; 8 in three rows or anterior row curving so strongly procurved that posterior margin of ALE is anterior to margin of AME. Group front width: back width: length, 64: 54: 42; ocular quadrangle of AME and ALE, front width: back width: length, 40: 20: 15; MOQ front width: back width: length, 33: 35: 26. AME: ALE: PME: PLE, 17: 16: 9: 11. Interspaces as AME diameters: AME-AME, 0.59; ALE-ALE, 2.0; PME-PME, 1.41; PME-PLE, 0.24. AME and PME only on low tubercle. Back row recurved.

*Chelicerae*. Robust, but from above curving gently to tip. Ental band of few long bristles and sparse golden or silver hairs, band narrow and widest posteriorly. Rastellum with distal line of 6-8 strong curved spines not on mound to about midpoint of fang joint, above that, roughly triangular area of longer and slightly thinner spines. Promargin with 7 large teeth similarly but not equally spaced, basal half of furrow with 6 small and 2 even smaller teeth along retrobasal edge.

*Labium*. 0.84 wider, 1.28 long, roughly triangular, no cuspules, anteriorly indented, cluster of long curved bristles on anterior lateral corners.

*Maxillae*. Front width: back width: length, 1.94, 2.81, 1.31; anterior lobe indistinct, inner edge concave with *ca.* 20 blunt cuspules clustered in anterior inner corner; heel projects posteriorly over labium and sternum; uniform cover of long curved bristles.

*Sternum*. 4.44 long, 3.13 wide. Posterior sigilla oval 0.44 long, 0.31 from margin. Ovoid, extends short distance between coxae IV. 3 pairs of sigilla; short fine brown hairs between sigilla and margin; long brown bristles centrally on sternum. Posterior sigilla ovoid, one length from margin.

*Legs*. Coxae I, II with slight heel. Legs I, II more slender and lighter built than III, IV. Tibiae and metatarsi IV with flat asetose but hirsute retrolateral face. At least 1 long erect seta on dorsal band on tibiae-tarsi I, II. Retrobasally on femur IV short group of (basifemoral) thorns in 2-3 bands; absent on I-III.

*Leg measurements* (femur to tarsus, total). Leg 1: 5.00, 3.38, 3.31, 2.94, 1.69; 16.32. Leg 2: 4.38, 3.06, 2.88, 2.50, 1.50; 14.32. Leg 3: 3.56, 2.44, 1.94, 2.44, 1.56; 11.94. Leg 4: 4.88, 3.50, 4.75, 3.94, 1.88; 18.95. Palp: 3.63, 2.13, 2.38, 2.38; 10.52. Leg ratios: I, 2.14; II, 1.88; III, 1.56; IV, 2.48.

*Scopula*. Dense on palpal tarsus, longest prolaterally; on tarsi I, II, distal 3/4 metatarsus I, 2/3 metatarsus II, absent on III, IV.

*Spines*. Absent on tarsi I, 2-3 ventrally on tarsi II. Prodistal knuckle of *ca.* strong bristles on femur IV. I: fe basal d2 bristles; pa p2; ti p1.1v1.1.2; me v 1.2.2. II: fe as I; pa p1.1; ti p1.1.v1.1.1; me p1 basal v2.2.2; ta v2-3. III: fe, 0; pa 8 long thorn setae prolaterally + 2 dorsal bristles; ti p1.1.r1.1.1.v2.2.3; me p1.1.1.2r1.1.1.v2.2.1.5; ta p1v12. IV: fe with knuckle; pa 15-20 short strong bristles opposing femoral knuckle; ti p0r1.1.1.1.v2.2.2w; me p0r1.1.1.v2.2.1.3.1.1.4; ta v15. Palp: fe and pa, 0; ti p2v2.2.3; ta v2 basal.

*Trichobothria*. *ca*. 8 per row basally on tibiae in sigmoidal lines converging distally at half length of tibia; *ca*. 14 basally on metatarsi in line but basally on retrolateral face and distal 6 staggered irregularly; tarsus with *ca*. 14 staggered irregularly, intermixed with setae, with no regular pattern of distribution. Tarsal organ subdistal, off centre line.

*Claws*. Palp with 1 long tooth basally, 3 small teeth to midlength on ental margin. Third claw long, curved, bare. Paired claws: I basally with bifid tooth, at midlength 3-4 smaller close together on ental edge, more on anterior claw; II, likewise with 5 on anterior claw, 3 on posterior claw and single basal tooth; IV with 2 large basal, anterior claw has 2 small teeth slightly distal of those, posterior claw has 2 basal and 3 very small on definite ental face.

*Abdomen*. Book-lung comb present, apertures narrow, slit-like.

*Spinerets*. PMS almost as wide as long but large; 0.53 long, 0.47 wide. PLS: basal 1.25 long, 0.75 wide at midpoint; middle and apical, articles 0.31, 0.19, long respectively.

VARIABILITY. The spines on the RTA form distinct transverse lines or ranks. The number of ranks of spines on the RTA and the number of spines in each rank varies between localities, some even in adjacent localities. In the holotype, there are only 4 straight continuous ranks with broken or discontinuous ranks basal and a distal cluster (Fig. 2C). However, in QMS54307 from Mt Tamborine, the number of ranks is closer to 9 plus 3 wide basal ranks and a distal cluster (Fig. 4F). Nevertheless, in all males included in *A. longipes*, the RTA spines are in ranks, there are few or no spines on tarsi I, II, and there are no true spines but at most strong bristles on the cymbium.

Although some males show strong similarity to the holotype in the palpal spination and are of similar size, only males from west of Brisbane at Camira and Flinton Hill (Ipswich) corresponded completely in size, palpal spination, and scopula on tarsi IV.

Abdominal pattern also shows some variability but usually the abdomen is ventrally pallid; however, males from Bahr's Scrub just south of Brisbane are darker dorsally and have brown flecks lateroventrally and the posterior booklung covers have a brown edging anteriorly.

DISTRIBUTION. SEQld to NE NSW; best knowledge is of localities south of the Brisbane River from Capalaba to Ipswich. Records north of the Brisbane River are limited: Brookfield, Enogerra, Toowong, and the most northerly locality at Beerwah.

HABITAT. Spiders were found in the most marginal and disturbed habitat adjacent to industrial areas, in suburban Brisbane, open forest on clay or sand, semi-evergreen vine thickets, rainforest and roadside verges adjacent to paddocks. They were most numerous on roadside verges adjacent to rainforest. Spiders were generally found in lowland areas but occur at least at Mt Superbus (870m), Mt Tamborine (670m.), and Beechmont (450m.), and they approach the elevation at which the sister species (*A. robertcollinsi*, sp. nov., 950m.) is known. Significantly, the latter two locations are simply the "lower" slopes of the same mountain range that rises to be capped by *A. robertcollinsi*.

This broad diversity of habitat of an idiopid mygalomorph contradicts conventional wisdom (e.g., Main, 1981) about idiopids which have to date been considered highly restricted in their habitat preferences. Equally, the differences in burrow entrance (below), especially with respect to use of leaves in the collar, have not before been reported in Australian idiopids.

PHENOLOGY. On attaining maturity (see Conservation, below), males wander in search of females with which to mate. Almost all records of male activity are derived from pitfall trap data where any one collection date spans from 1 to 8 months. To use these data, one unit was assigned to each male found in each month of the potential collection period; hence, one male taken in pitfall traps set from April to January contributes 8 units. A total of units shows the likelihood of male activity: lowest was from June 1 to October 1 (4 months, 16 units); from October to May, the three contiguous month likelihood ranged from 21-44 units, mode 32; from October to March, the mode was 40. Hence, males are active yearlong (two males were taken in July and August) but highest activity occurs in summer from November to April. In contrast, over 50% of males of the sister species, *A. robertcollinsi*, sp. nov., were taken between April and June.

CONSERVATION. Mygalomorphs are univoltine, long-lived and highly sedentary animals. What little we know of their biology is deduced from studies of few species, some unpublished. An egg sac is made in the burrow. The young emerge, remain in the maternal burrow for one or two moults and then disperse

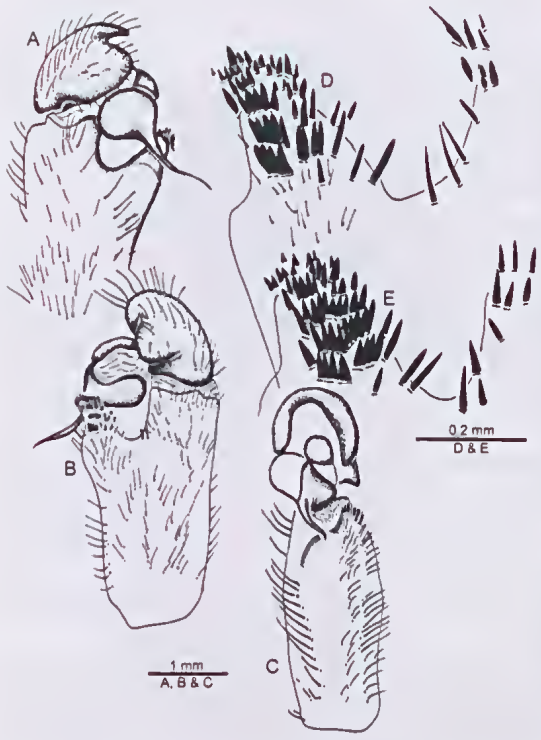


FIG. 6. *Arbanitis robertcollinsi*, sp. nov., palpal tibia, RTA, tarsus and bulb, male. A-C, prolateral (A), retrolateral (B), and ventral (C) views; D, E, RTA, retrolateral view at different angles.

very nearby and make their burrow. Spiders mature after 5-7 years during which time all make similar burrows. The female remains in the burrow, enlarges it and moults each year. The male, once adult, leaves the burrow and wanders in search of the female, mates and is either eaten by the female or dies soon after. Females of larger species (e.g., Theraphosidae, large Hexathelidae) live for over 20 years. Judged on size alone, females of *A. longipes* probably live at most 10 years, possibly longer in rainforest from where larger females are known.

The proximity of *A. longipes* to large and growing urban areas of Brisbane and Ipswich raises concerns about its viability. It is important here to distinguish between presence of live adults and a viable population. Remarkably, Toowong is deep in the heart of suburban Brisbane and a female was collected in 1989.

BURROW. Females build a short (8-20cm long) sinuous burrow without a door or tube-like extension; in some burrows, the burrow is Y-shaped (as in the nemesiid *Aname*; Raven, 1981). The second "entrance" in the burrow of one female (QM S 8977) measured was 7-8cm from the main entrance and just below the soil, i.e., a thin layer of soil obscured the opening. The two tubes joined at 12-15 cm depth and a short shaft continued below that for *ca.* 5 cm. The burrow entrance is only slightly raised above the ground and inclined at about 30° to the horizontal (Figs 1C, D). In many burrows seen (by RR), especially smaller spiders, the entrance lacked leaves. Leaves were bound into burrow entrances (Fig. 1D) of larger females found on the top of embankments at Pine Mt. Burrows were found on flat or almost flat ground as well as on slopes and roadside cuttings. On embankments up to 1 metre high, burrows were more numerous (*ca.* 5 in 30x30cm square) on the upper than lower half and were most numerous (up to 20 in 30x30cm square) at the top of the embankment and close behind it on the flatter slope.

Burrows were found in areas of exposed earth most commonly with little leaf cover and in slopes of any aspect to the sun . No burrows were found where the leaf litter was dense (i.e., leaf fall was high). On gentle slopes, burrows showed strong clumping—burrows of juveniles were clustered within 30cm of a larger burrow, presumably that of the maternal female.

The burrow silk contrasted to that seen in other *Arbanitis* species. Silk at the burrow entrance of larger females was thick but silk *ca.* 1-3 cm (i.e., more with larger spiders) below that was very thin, fine and white but not concealing the spider, not adhering to the edge of the tube, and easily broken or torn—much like that in the diplurid *Australothele*.

Unlike the Tube-spiders (e.g., *Misgolas robertsi*, *M. mascordi*), which build an extended aerial tube (not unlike that built by the Palaearctic *Atypus* but with an opening), females of *A. longipes* do not raise the burrow off the ground to any extent. The most elevated seen were those on the crest of embankments in which extension is exaggerated by the slope.

SYMPATRIC MYGALOMORPHS. The Queensland Museum database was checked for other mygalomorphs which were taken in areas contiguous with, adjacent to, or including those in which material of *A. longipes* was taken, i.e., they could be taken to be sympatric. (*A. longipes* was also recorded from greater Brisbane.) Eleven such localities were identifiable; all localities had

been surveyed for at least 1 year, if not longer, or the mygalomorphs were well known. Of those, diversity varied from 3 species in 3 families (Bahrs Scrub) to 16 species in 7 families at Mt Tamborine.

REMARKS. Although the published type locality of *Arbanitis longipes* is "Bowen", Queensland, the only material closely matching the holotype are from areas around Brisbane. The possibility that an as yet undiscovered population of *A. longipes* may be found near Bowen cannot be dismissed completely. However, we examined all collections of Australian museums for idiopids with no spur and spines in lines on the palpal tibial apophysis of males—the minimum qualifying characters for *A. longipes*. That search yielded only the material listed here. All male idiopids from the Bowen region in the QM collection have a tibial spur and the spines on the tibial apophysis do not closely resemble the lines in *A. longipes*. Equally, no other spider species yet known has a distribution that includes only the Brisbane area and Bowen. As indicated above, a very close match of new material from Camira with the holotype makes the issue conclusive. Hence, we consider that the type-locality is incorrect, not unknown in the Godeffroy material (e.g., Raven, 1982), and was presumably "Brisbane" but most precisely is Camira on the Brisbane-Ipswich civic boundary.

**Arbanitis robertcollinsi**, sp. nov.
(Figs 5E, 6, 7, 12, 13)

MATERIAL. HOLOTYPE: QMS28822, ♂, Springbrook Repeater Station, 28°14'S 153°16'E, SE.QLD, rainforest, intercept flight trap, 14 Mar 1997-15 May 1997, G Monteith. PARATYPES. QLD: Lamington National Park, rainforest, SE.Q. Allotype: QMS54321, ♀, Binna Burra Lodge, 28°11'S 153°11'E, SE.QLD, rainforest, 19-20 May 2003, R.J. Raven; QMS54322, ♀, same data as S54321; QMS31798, S42712, 3 ♂♂, Echo Point, 28°15'S 153°10'E, pitfall, 24 Mar-24 May 1992, G Monteith; QMW2390, ♂, 22 May 1963, G Monteith; QM S20684, 2 ♂♂, Eeho Point, pitfall, 27 Dec 1991-24 Mar 1992, G Monteith; QMS8932, 13 ♂♂, O'Reillys, 28°13'S 153°08'E, Apr-Jun 1982, G Monteith; QM S8983, 2 ♂♂, O'Reillys, pitfall, 15 Jan-4 Feb 1982, G Monteith, D. Yeates; QMS9074, ♂, O'Reillys, pitfall, 28 Sep 1975-31 Jan 1976, G & S. Monteith; QM S8966, S9031, 3 ♂♂ [2 ♀♀], O'Reillys, Wishing Tree Circuit, 28°14'S 153°08'E, pitfall, 27 Dec 1981-15 Jan 1982, G Monteith, R. Raven. D. Yeates; QM S54306, ♂, Springbrook Repeater, 28°14'S 153°16'E, intereept flight trap, 9 Jan-19 Feb 1995, G Monteith; QMS48460, ♂, Tullawallal, Binna Burra, 28°12'S 153°11'E, pitfall, 9 Jan-6 Apr 1995, G Monteith. NSW: AM KS 48903: McPherson Range, 28°22'S, 152°45'E, 550m, H. Smith. Hines Pugh Webber, pitfall trap (T2.29), 22 Feb 1989, Mt Warning Caldera Survey, University of New England.

DIAGNOSIS. Males differ from those of *A. longipes* in having a pronounced mound at the base of RTA and the spines on the RTA are not in such clearly spaced ranks, especially near the tip of the RTA.

DESCRIPTION HOLOTYPE ♂. *Colour in alcohol.* Carapace orange brown, eyes with black edges but entire region not dark; chelicerae dark red brown. Abdomen dorsally fawn with irregular brown flecks; ventrally without pattern. Legs orange brown, lateral with slightly darker "burnt" area on patellae I and II only.

*Carapace.* Broken lines of silver hair on interstrial ridges and caput ridge. Margins with band of 2-3 irregular lines of short black thick curved bristles. Fovea wide, straight with recurved edges; 2-3 pairs weak foveal bristles. Four short weak anteromedial bristles.

*Eyes.* Front row slightly wider than straight back row.

*Chelicerae.* Rastellum soil-encrusted, strong: line of 5 short thick spines from inner edge to half fang width; no spines above basal group on inner cheliceral edge. Fangs long without outer keels or ridges, no serrations on ventral keel. Furrow promargin with 8 irregularly spaced teeth, retrobasal line of 4 larger distal and group of 2 basal rows of 6 smaller teeth.

*Labium, maxillae.* Like *A. longipes*. Labiosternal sigilla narrows medially to form tear-shaped sigilla with low adjacent sternal edge.

*Sternum.* Sigilla: all oval. With many fine setae uniformly mixed with bristles.

*Scopula.* Scopulate areas of I, II amost asetose, pallid. Long hairs, moderately dense, and extending to lateral edges for distal half of metatarsi I, II; scattered hairs only on III. Dense, full, entire but short on tarsi I, II, distal and entire III, IV.

*Spines.* I: fe p1d1 1w; pa p1v1; ti p4v3.2.1.3; me p1v3.1.1; ta 0. II: fe p5d4r1; pa p2; ti p4v7; me p1v1.2.1.1.2; ta 0. III: fe p2d3r2; pa p7r1; ti p4r3v2.2.3; me p5r4v2.1.1.4; ta p2rv1. IV: fe r2; pa 0; ti r5 (long) v3.2.2; me r4v2.1.1.2.1.4; ta p2rv3. Palp: fe 0; pa p2; ti only on process; ta 0.

*Claws.* I: STC with long sinuous row from distally ental to basally mesal; all teeth of similar size but basal 2 penultimate teeth longer; ITC slightly curved, bare. IV: short curved row of 4 similar teeth entally, clearly separated from basal pair of two larger teeth.

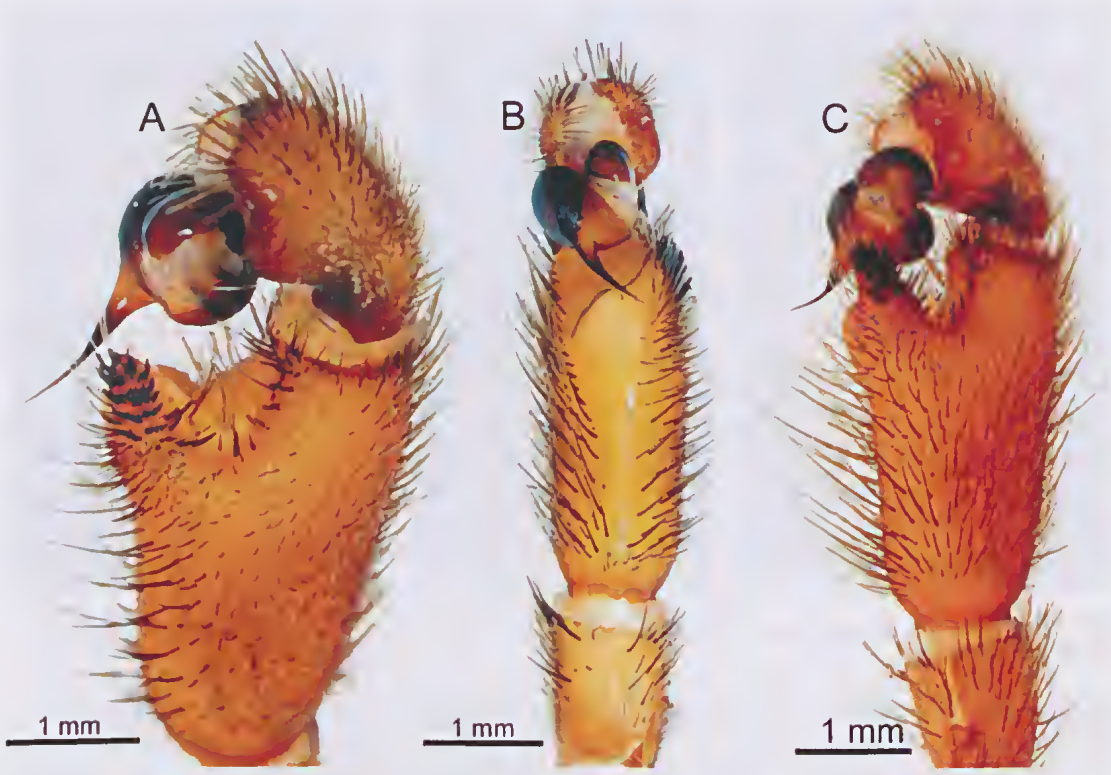


FIG. 7. *Arbanitis robertcollinsi*, sp. nov., palpal tibia, RTA, tarsus and bulb, male. A, C, retrolateral views; B, ventral view.

*Palp*. Tibia slightly flattened laterally with strong distally directed RTA in apical third; process lies within line off end of tibia; ventral half of tibia and inner edge of process glabrous; inner base of process with distinct ental mound; in distal half with 5 ranks of long blunt spines, in each rank spines in rosettes of 4, basal rank more separated than others, each rank with 8-10 digitiform pairs, 3-4 long spines on basal process, 4 in rough line in short curve and 2 groups each with 3 distally; embolus with simple filiform tip. Cymbium aspinose.

♀. Unable to be reliably matched to male.

REMARKS. One species of *Arbanitis* and three species of *Misgolas* are known from the Lamington National park. We cannot be sure which female matches the male until we have biological data or collect a female live, get its DNA checked against *A. robertcollinsi* and then describe it or compare it to the one described here.

ETYMOLOGY. For Robert Collins, who first pressed for the designation of the McPherson Range area as a national park.

DISTRIBUTION. Known only from Lamington National Park, SE.Q.

**Arbanitis beaury**, sp. nov.
(Figs 8, 12, 13)

DIAGNOSIS. Differs from *A. longipes* in lacking prolateral spines on femora I, II and spines on tarsi II and patellae I, II and from *A. robertcollinsi* in having spinules on the cymbium, also the spines on the RTA are all long but not in such distinct ranks as in *A. longipes*.

MATERIAL. HOLOTYPE: AM KS48641, M, Beaury State Forest, 28°33'S 152°19'E, 4 Feb-9 Apr 1993, M. Gray, G. Cassis.

OTHER MATERIAL. AM KS 36693, M, Boonoo State Forest, Boonoo Forest Drive, 1.8k from Mt Lindsay Highway, 28°56'S 152°06'E, M. Gray, G. Cassis, 4 Feb-9 Apr 1993. KS36694, Boorook State Forest, M [and pM nontype], midway between Boorook and Gilgurry Cks on

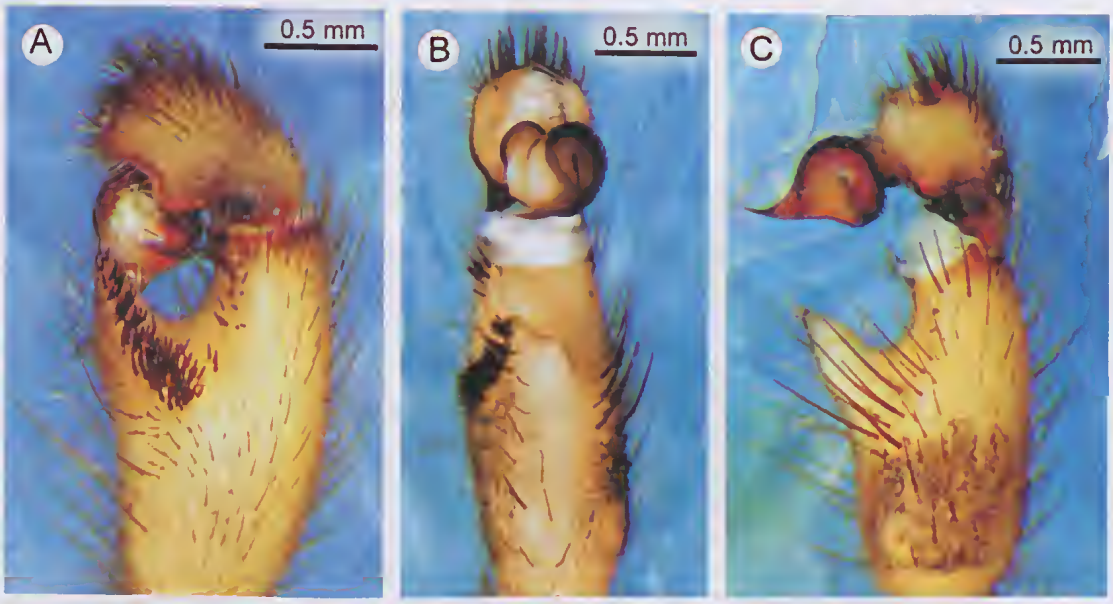


FIG. 8. *Arbanitis beaury*, sp. nov., palpal tibia, RTA, tarsus and bulb, male. A, retrolateral views; B, ventral view; C, prolateral view.

Conlogan Rd, 1km NW Boorook Ck junction, 28°51'S 152°11'E, M. Gray, G. Cassis, 4 Feb-3 Apr 1993.

DESCRIPTION Holotype ♂ AMKS48641. As for *A. longipes* except:

*Colour in alcohol*. Carapace dark orange brown with darker reticulated areas on caput and interstrial ridges, eyes with black edges; chelicerae dark orange brown. Abdomen dorsally brown with full length pallid widening in distal quarter, 3 paired pallid spots with area of fourth pair broken laterally between, each pair a diagonal pallid stripe; no pattern ventrally. Sternum, maxillae and labium yellow brown, sternum with dark triangular area medially for length. Basal PMS ventrally and laterally and lateral PLS brown. Legs orange brown with burnt brown patches: femur 1 for distal fifth, patella, tibia and metatarsi I pro- and retrolaterally for length, lighter on metatarsi; leg 2 like 1 but not as dark, and only for distal two-thirds retrolaterally on patella; none on legs 3; femur 4 light brown prolaterally for distal sixth, for prolateral length but only distal third retrolaterally on patella, and paler on prolateral tibia; on palp, basal and distal femora, distal third pro- and retrolaterally on patella, pro- and retrolaterally on tibia and basal cymbium with brown collar.

*Carapace*. Light pile of long silver hair on interstrial ridges and caput. Margins with band of 2-3 irregular lines of short black thick curved bristles. Few weak bristles on posterior pair of interstrial ridges. Fovea wide, with recurved edges. Large recurved bristle between AME, smaller curved one between PME.

*Chelicerae*. Long, slender with long triangular band of long bristles for length. Rastellum strong: line of 5 short thick spines from inner edge about half of fang edge. Intercheliceral tumescence a moderately large rhomboidal pallid area. Furrow promargin with 6 small spaced teeth, retrobasally a line of 6 smaller teeth ending at mid-length of prolateral row.

*Maxillae*. Long, with rounded heel with *ca*. 15 lanceolate cuspules on anterior inner edge.

*Labium*. Labiosternal groove with two separate triangular sigilla.

Legs. Metatarsi and tarsi I, and tarsi II straight.

*Scopula*. Scopulate areas of I, II pallid. Entire for distal half of metatarsi I, II. Dense, full, entire but short on tarsi I, II, absent on III, IV.

*Spines*. Line of strong blunt bristles on prodistal edge of femur III. I: fe d5w; pa 0; ti p2v2.2.3; me v2.2; ta 0. II: fe d4; pa 0; ti p2v2.2.3; me v1.1.1.2; ta 0. III: fe d3w; pa p1.2.1.2.2 all long thorns; ti p2d2r2v1.2.3; me p2r3v2.2.1.4; ta pv2v1rv2. IV: fe d4r4; pa 0; ti r5 in line v2.2.2; me p1r3v.2.2.1.5; ta pv5rv3. Palp: fe d4w; pa 0; ti only on process; ta with long spinules.

*Palp*. Tibia as for *A. longipes* but ventral half of tibia and inner edge of process paler, weakly sclerotised. RTA broad, basally swollen with distinct pallid setose mound, conical with 2 staggered bands of long spines retrolaterally and confined to ventral edge; spines *ca*. 5-7 times longer than wide. Spines in lines from RTA tip to base: 3,6,8,5+6,4+6, basally with 5 then 3 in irregular curving line; in prolateral edge of tibia 2 basal at RTA base then 1.1.1.1.2.1 in distal ridge. Cymbium with *ca*. 8-10 thick bristles or spinules anteriorly. Embolus wide.

ETYMOLOGY. From the type locality.

DISTRIBUTION & HABITAT. Known only from Beaury, Boonoo Boonoo and Boorook State Forests, northern New South Wales.

### **Misgolas** Karsch, 1878

*Misgolas* Karsch, 1878: 821. Type species by monotypy, *Misgolas rapax* Karsch, 1878.

*Hermeas* Karsch, 1878: 823. Type species by monotypy, *Hermeas crispus* Karsch, 1878. First synonymised with *Misgolas* by Main, 1985. Note: unknown to Raven (1985) who also noted the synonymy (but used *Hermeas* instead). Main chose *Misgolas* as the senior name and assumed, contrary to the International Code of Zoological Nomenclature, that page precedence was the sole determinant of priority. In so doing, Main selected a type species that was difficult to diagnose from the other four sympatric congeners. Main's designation preceeded that of Raven.

*Dyarcyops* Hogg, 1902: 130. Type species by original designation, *Dyarcyops andrewsi* Hogg, 1902. First synonymised by Main, 1985.

*Megalosara* Rainbow, 1914: 205. Type species by monotypy: *Megalosara villosa* Rainbow, 1914. First synonymised by Main, 1985.

DIAGNOSIS. Differs from *Arbanitis* in the pointed conical lobe on the retrolateral cymbium of males, the adorned (with flanges, or serrate keels) embolus and the presence of a distal process retrolaterally on the palpal tibia of males.

SPECIES INCLUDED.

*Dyarcyops andrewsi* Hogg, 1902
*Dyarcyops birvi* Kulczynski, 1908
*Hermeas crispus* Karsch, 1878
*Misgolas dereki* Wishart, 1992
*Arbanitis elegans* Rainbow & Pulleine, 1918
*Arbanitis gracilis* Rainbow & Pulleine, 1918
*Arbanitis hirsutus* Rainbow & Pulleine, 1918
*Cantuaria hoggi* Simon, 1908
*Misgolas hubbardi* Wishart, 1992
*Misgolas kirstiae* Wishart, 1992
*Dyarcyops maculosus* Rainbow & Pulleine, 1918
*Misgolas mascordi* Wishart, 1992
*Arbanitis mestoni* Hickman, 1928
*Idioctis ornata* Rainbow, 1914
*Arbanitis papillosus* Rainbow & Pulleine, 1918
*Misgolas rapax* Karsch, 1878
*Dyarcyops robertsi* Main & Mascord, 1974
*Arbanitis villosus* Rainbow, 1920

SPECIES RESTORED TO *CANTUARIA* FROM *MISGOLAS*

*Cantuaria abditus* Forster, 1968
*Cantuaria allani* Forster, 1968
*Cantuaria apertus* Forster, 1968
*Cantuaria apicus* Forster, 1968
*Cantuaria assimilis* Forster, 1968
*Cantuaria borealis* Forster, 1968
*Cantuaria catlinensis* Forster, 1968
*Cantuaria cognatus* Forster, 1968
*Arbanitis collensis* Todd, 1945
*Cantuaria delli* Forster, 1968
*Maoriana dendyi* Hogg, 1901
*Cantuaria depressus* Forster, 1968
*Cantuaria dunedinensis* Forster, 1968
*Nemesia gilliesi* O. P.-Cambridge, 1878
*Cantuaria grandis* Forster, 1968
*Arbanitis huttoni* O. P.-Cambridge, 1879
*Cantuaria insulanus* Forster, 1968
*Cantuaria isolatus* Forster, 1968
*Cantuaria johnsi* Forster, 1968
*Cantuaria kakahuensis* Forster, 1968
*Cantuaria lomasi* Forster, 1968
*Cantuaria magnus* Forster, 1968
*Arbanitis marplesi* Todd, 1945
*Cantuaria maximus* Forster, 1968
*Cantuaria medialis* Forster, 1968
*Cantuaria minor* Forster, 1968
*Cantuaria myersi* Forster, 1968
*Cantuaria napua* Forster, 1968
*Cantuaria orepukiensis* Forster, 1968
*Cantuaria parrotti* Forster, 1968
*Cantuaria pilama* Forster, 1968
*Cantuaria prina* Forster, 1968
*Cantuaria reductus* Forster, 1968
*Cantuaria secundus* Forster, 1968
*Cantuaria sinclairi* Forster, 1968
*Cantuaria stephenensis* Forster, 1968
*Arbanitis stewarti* Todd, 1945
*Cantuaria sylvaticus* Forster, 1968
*Cantuaria toddae* Forster, 1968
*Cantuaria vellosus* Forster, 1968
*Korua wanganuiensis* Todd, 1945

DISTRIBUTION. Australia.

REMARKS. All New Zealand species are restored to *Cantuaria*.

### **Misgolas bithongabel** sp. nov.
(Figs 9, 12, 13)

MATERIAL EXAMINED. HOLOTYPE: QM S9090, ♂, Mt Bithongabel, 28°15'S 153°10'E, 27 Sep 1975-31 Jan 1976, G. & S. Monteith. Paratype: QM S35397, ♂, O'Reillys, 28°13'S 153°08'E, 15 Jan-4 Feb 1982, G.

FIG. 9. *Misgolas bithongabel*, sp. nov., leg I, palpal tibia, RTA, tarsus and bulb, male. A-C, retrolateral views; D, tibia, metatarsus and tarsus I, prolateral view.

Monteith, D. Yeates. Both taken in pitfall in rainforest, in Lamington National Park, SE.Qld.

DIAGNOSIS. Differs from the sympatric *Arbanitis longipes* by a pair of megaspines forming the coupling spur on tibia I of males and disordered spines on the palpal tibial apophysis. No other males of described *Misgolas* or *Arbanitis* species have a tibial spur in this simple form.

DESCRIPTION. Holotype ♂, QM S9090; like *A. longipes* except as follows.

Carapace 5.50 long, 4.56 wide. Abdomen 5.62 long, 3.62 wide. Total length, 9.

*Colour in alcohol*. Carapace and legs orange brown; legs without darker zones. Abdomen dorsally brown with five pairs of oval (anterior pairs) to slit-like (posterior pair) pallid areas; laterally mottled brown fading to almost entirely pallid ventrally save for irregular brown bar at posterior third.

*Carapace*. With uniform light cover of long fine white hairs ; 10-15 anteromedial bristles, 6-8 pairs of bristles posteriorly directed on posterior caput edge; strong bristles only on margins and between posterior striae.

*Eyes*. Group front width: back width: length, 44:40:22; anterior ocular quadrangle front width: back width: length, 44: 22: 10. AME: ALE: PME: PLE, 9: 10: 4: 8. Interspaces as AME diameter: AME-AME, 0.6; AME-ALE, 0.4.

*Chelicerae*. Short, almost geniculate with wide hirsute band of bristles entally and narrow ectal band. Distinct rastellum extends from mid-front entally in slightly diagonal line of 5 long thick spines and 1-3 smaller spines entally. Intercheliceral tumescence a moderately large pallid area. Teeth on furrow promargin; hardened formalin fixation prevents seeing more detail without destroying chelicera.

*Maxillae*. With *ca*. 20 lanceolate cuspules.

*Legs*. Tibia I prolaterally with coupling spur of two spine groups: upper with long curved dorsal spine strongly truncated (one side also has scar if second lower spine) on very low mound; low conical mound ventrally with large single apical tapering spine and smaller on edge of spur. Metatarsi and tarsi I, and tarsi II gently dorsoventrally bowed; metatarsi I broadened ventrally.

*Scopula*. As for *A. longipes* but, dense, full, entire but hairs short on tarsi I-IV.

*Spines*. All pedal tarsi aspinose. I: fe d4w; pa0; ti v1.1.2 + megaspines; me rv1 basal weak. II: fe d2w; pa 0; ti v1.1.2; me v1. III: fe d2w; pa p2.2.4 thorns; ti p2r2v1.1.1; me p2r2v0. IV: fe d3wr4w + 8 in line in distal comb (spines only *ca*. 3 times longer than wide) opposed by 6 similar on probasal patella; ti p0r0v1.1.2; me r1rv1.1.1. Palp: fe 0; pa 0; ti only on RTA; cymbium, see Palp.

*Claws*. 4-5 long teeth on cntal face of I, IV, 2 larger teeth on basal midline.

*Palp*. Tibia slightly flattened laterally with strong distally directed RTA in apical third; RTA about as long as wide at base; inner base of RTA gradually joins tibia ventrally; distinct unsclerotised asetose conical mound at base of RTA pointed ventrally. Process broad, triangular with *ca*. 39 spines on RTA and adjacent ridge. On RTA, spine shape varies from *ca*. 1.5-3 times longer than basal width; spines only on retrolateral and distal faces; one irregular line of basally, more distad a roughly circular area of *ca*. 23 spines uniformly placed but in no evident order, 4 in line distal of that and apically on process, a cluster of 5-6. Secondary apophysis low but with distinct lobe and 6-8 longer spines point basally toward RTA and 3 smaller spines distal of that; valley between two apophyses

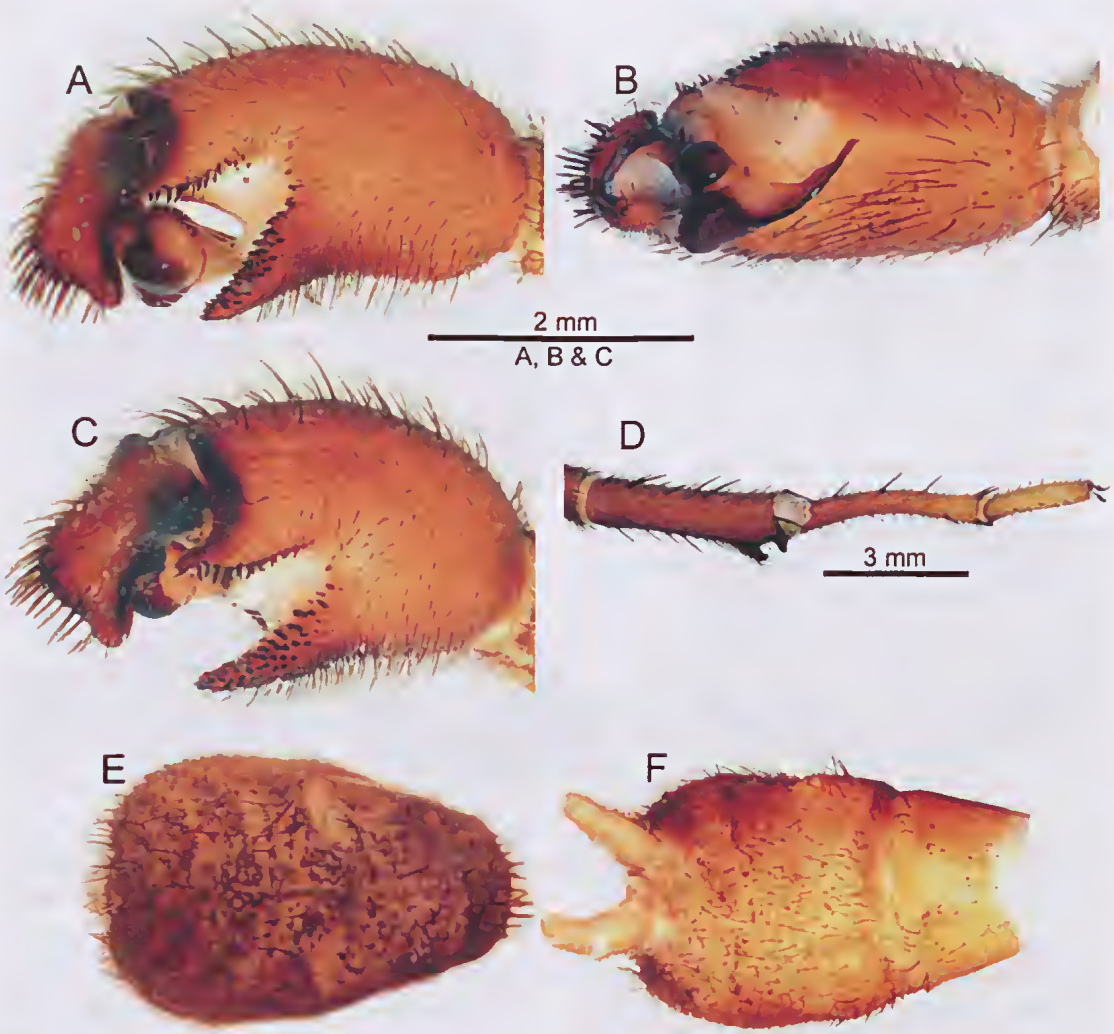


FIG. 10. *Misgolas echo*, sp. nov., palpal tibia, RTA, tarsus and bulb, male. A-C, retrolateral views; D, tibia, metatarsus and tarsus I, prolateral view; E, abdomen, dorsal view; F, abdomen, ventral view.

short (less than basal width of RTA) with 3 longer spines opposed by long spines on secondary apophysis; otherwise short trianguloid thorn-like spines uniformly spread over almost flat triangular area. Cymbium with cluster of broad flat spines in distomedial triangle; acute retrolateral lobe forms angle of *ca.* 60°. Bulb pyriform with large slender median haematodocha extending to narrow base of embolus. Embolus with 8 small serrations, 2 of which terminate low keels off bulb.

*Posterior Book-lungs*. Covers 1.17 wide, 0.92 long; aperture 0.42 wide, 0.08 deep.

ETYMOLOGY. From the type locality.

BURROW. Conclusive recognition of the burrow of *M. bithongabel* has not been possible. However, throughout the region, a second distinctive burrow type that a likely candidate for the female is recognisable; it is the elevated tube usually attached to small saplings. The tubes are now seen more rarely than in 1970-1980 when Raven's attempt to trap the spider without major excavation was unsuccessful.

DISTRIBUTION & HABITAT. Rainforest at Lamington National Park, SE.Q.

**Misgolas echo**, sp. nov.
(Figs 10)

MATERIAL EXAMINED. HOLOTYPE: QM S20629, Lamington NP, Echo Point, 28°15'S 153°10'E, SE.QLD, rainforest, intercept flight trap, 27 Dec 1991-24 Mar 1992, G. Monteith. Paratypes: QM S46399, 3 same data but 24 Mar-24 May 1992, G. Monteith; QM S9054, male, Lamington Plateau, Lookout Point, 28°15'S 153°08'E, SE.QLD, rainforest, 30 Nov 1976, R. Freeman. QM S9340, Upper Tallebudgera Valley, 28°14'S 153°16'E, SE.QLD, rainforest, Mar-Jul 1985, D.J. Cook; QM S15424, Nothofagus Mt, 12km N Woodenbong, 28°17'S 152°36'E, NE.NSW, rainforest, pitfall, 1981-1982, G. Monteith; QM S8928, Victoria Pk, via Alstonville, 28°53'S 153°22'E, NSW, rainforest, pitfall, 23 Mar-3 Aug 1975; QM S9102, same data but 3 Aug-16 Nov 1975, G. & S. Monteith. QM S9181, Upper Tallebudgera Valley, 28°14'S 153°16'E, SE.QLD, rainforest, pitfall, 8 Jan-17 Mar 1985, G. Monteith, G. Thompson, D. Cook.

DIAGNOSIS. Males differ from those of *M. monteithi* and other described males of *Misgolas* in the triangular secondary apophysis on the palpal tibia and from *M. bithongabel*, sp. nov. in the strong coupling spur on tibia I.

DESCRIPTION. Holotype QM S20629. *Colour in alcohol.* Carapace orange brown, eyes with black edges but entire region not dark; chelicerae darker. Abdomen dorsally fawn with irregular brown flecks forming one anterior large paired and two small larger paired pallid zones; ventrally pallid with few brown spots forming irregular median band. Legs orange brown, without darker areas.

*Carapace.* Almost glabrous, few silver hairs intermixed with short bristles on interstrial ridges and caput ridge; 3 strong bristles in posterior striae and broad band along posterior carapace margin. Lateral margins with single line of short strong black curved bristles. Fovea wide, straight. Seven short weak anteromedial bristles. Three long recurved bristles in front of AME.

*Eyes.* Front row wider than back row.

*Chelicerae.* Rastellum strong: line of 4-5 short thick spines from inner edge to half fang width, two smaller but thick conical spines laterally and 4 above spines on inner corner along inner cheliceral edge. Furrow promargin with 9 irregularly spaced teeth, retrobasally for basal half a line of 4 larger distal and 3 smaller teeth basally. Interchelical tumescence not evident.

*Labium, maxillae.* Like *A. longipes*. Labiosternal sigilla uniformly wide with folded adjacent sternal edge medially.

*Sternum.* Sigilla: all oval. Sparsely setose and almost devoid of hairs, except marginally.

*Legs.* Tibia I with medium-sized distal coupling spur with two conical spines on lower distal mound and 3 short, broad spines on subdistal lobe; metatarsus I distinctly bowed prolaterally deepest at basal third.

*Scopula.* Scopulate areas of I, II amost asetose, pallid. Long hairs, moderately dense, and extending to lateral edges for distal fifth of metatarsi I, II; scattered hairs only on III. Full, entire but short on tarsi I, II, absent on III, IV.

*Spines.* I: fe 0; pa 0; ti v1.2.2; me v1.1.1.1.3; ta pv6rv11. II: fe 0; pa 0; ti p2 v7; me p1 v2.2.1.2; ta pv6rv11. III: fe 0; pa p3; ti p2r2v1.1.4; me p3r3v10; ta pv8rv15. IV: fe d3wr3w; pa 0; ti r4v7; me r3v13; ta pv12rv13. Palp: fe 0; pa 0; ti only on process; ta *ca.* 25 long weak spines across distal dorsal half.

*Claws.* I: STC with long sinuous row from distally ental to basally mesal; all 9 teeth of similar size; ITC slightly curved, bare. IV: like I.

*Palp.* Tibia slightly flattened laterally with strong distally directed RTA in apical third; process lies within a line off end of tibia; ventral half of tibia and inner edge of process setose. Tibial apophysis conical, with slightly incrassate base anteriorly, forming sharp V-shaped groove with distal process; c.40 short blunt pointed spines forming no evident pattern over distal surface, very few in groove; distal process with distinct spinose rounded ridge with 3-4 large conical spines medially, 8 smaller spines distally and 15 basally; distal process forms tip; embolus with long grooved tip; unsclerotised ventral near base of tibial apopohysis with distinct unsclerotised ental mound bearing two long setae. Cymbium with distinctly narrowed retrolateral lobe with c.25 long spines over distal edge.

ETYMOLOGY. From the type locality.

DISTRIBUTION & HABITAT. Rainforest at Lamington National Park and Upper Tallebudgera Valley, SEQ, and Alstonville and Nothofagus Mt, near Woodenbong, NE NSW.

**Misgolas monteithi**, sp. nov.
(Figs 11)

MATERIAL EXAMINED. HOLOTYPE: QM S20675, ♂, Lamington NP, Pat's Bluff, 28°14'S 153°08'E, SE.QLD, open forest, 17 Nov 1991, G. Monteith.

DIAGNOSIS. A very large dark idiopid in which the males differ from those of the other species

FIG. 11. *Misgolas monteithi*, sp. nov., leg I, palpal tibia, RTA, tarsus and bulb, male. Retrolateral (A) and ventral (B) views; C-E, bulb, rotated views; F, G, tibia, metatarsus and tarsus I, ventral (F) and prolateral (G) views; H, abdomen, ventral view.

with a coupling spur on tibia I by the unique sinuous form of the secondary palpal apophysis (Fig. 11A, B).

DESCRIPTION HOLOTYPE ♂ QMS20675: like *M. echo* except as follows.

Carapace 8.20 long, 7.50 wide. Abdomen 7.90 long, 4.2 wide. Total length, 19.

*Colour in alcohol.* Carapace red brown; sternum, maxillae and labium orange to red-brown. Abdomen dorsally dark brown anteriorly with large median pale zone flanked by pair of smaller dots behind which are 5 pairs of thin transverse pallid bars; posterior book-lung covers orange between which is blue black zone; otherwise ventrally pallid with brown flecking laterally and less dense but evident medially. Legs red brown with burnt zones (less distinct than in *M. echo* prolaterally and retrolaterally on patellae I, II) without darker areas.

*Carapace.* Lightly hirsute; 3-5 strong bristles in posterior striae. Lateral margins with short strong curved black bristles in 1-2 irregular lines anteriorly and 3 posteriorly. Fovea wide, straight with recurved ends. Six short weak anteromedial bristles. Three long recurved bristles in front of AME, 2 on clypeal edge, 2 between PME.

*Eyes.* Group front width: back width: length, 59:50:36; anterior ocular quadrangle front width: back width: length, 59: 33: 20. AME: ALE: PME: PLE, 12: 14: 7: 10. Interspaces as AME diameter: AME-AME, 0.6; AME-ALE, 0.4

*Chelicerae.* Rastellum strong: line of 4-5 short thick spines from inner edge to half fang width and 4-5 thick conical spines 4 above those. Furrow promargin with 8 teeth, retrobasally for basal half a line of 8 larger distal and 3 smaller teeth basally. Interchelical tumescence a large ovoid area, pallid ventrally.

*Labium, maxillae*. Like *M. echo* but *ca.* 40 pointed cuspules in narrow band in anterior ental corner.

*Sternum*. Sigilla: all oval. Strong uniform cover of bristles and setae.

*Legs*. Tibia I with medium-sized distal coupling spur with two straight conical spines on lower distal mound and 2 short, broad sinuous spines on subdistal lobe; gap so formed = diameter of base of distal mound; metatarsus I slightly bowed laterally; tarsus IV bowed dorsoventrally.

*Scopula*. On tarsi I, II, dense, full, entire but short and weak for length of III, IV; on metatarsi I, II, dense for distal 5/6, and weak in distal sixth of III, IV.

*Spines*. I: fe d1w; pa 1w; ti p1v1.1.1.2; me v1.2.0; ta 0. II: fe p1d2w; pa p1; ti p2v2.1.1.2; me v1.3.1.1.1.3; ta pv0rv9. III: fe 0; pa p14 thorns; ti p2r3v2.2.4; me p3r5v2.2.1.2.2.1.1.4; ta pv9rv10. IV: fe d3w; pa 0; ti r7 in line v9w; me r4wv12 d4 strong; ta pv12rv13. Palp: fe 0; pa 0; ti only on process; ta *ca.* 25 long weak spines across distal dorsal half.

*Claws*. I: STC with long sinuous row with 4 distal shorter teeth and crest of 5 teeth basally: basal crest with smallest tooth basally, more distal teeth longer such that second basal already as long as distal group of 4 and distal 3 of crest longest and recurved. IV: like I but 3 in distal group and 4 in basal crest with most basal tooth absent.

*Palp*. Tibia barrel-shaped, laterally rounded, not flat. Small, slender pointed horn-like RTA distally concave, basally convex with distinct groove at secondary apophysis, secondary apophysis a curved (ventrally concave) sinuous horizontal ridge, basally with rounded mound narrowing quickly to saddle ridge then widens laterally and horizontally into ventrally flattened shield. Spines on RTA uniform in size, *ca.* 2-4 times longer than wide in broad triangular area only on distal concavity of RTA with 20-30 thorns apically; 10 coniform spines in valley; *ca.* 20 on ventral face of basal secondary apophysis and just onto distal ridge and 2-3 onto adjacent flat face. Cymbial lobe coniform; 20-30 long straight attenuate spines dorsally on cymbium. Bulb with small unsclerotised median haematodocha but continuous with weakly sclerotised area extending to embolus tip; embolus distally twisted, apically bifid, basal lobe and main lobe similar.

*Spinnerets*. *ca.* 10 large pumpikiniform spigots on PMS, less on basal and middle segments of PLS.

*Posterior Book-lungs*. Covers 2.00 wide, 1.50 long; aperture 1.17 wide, 0.10 deep.

DISTRIBUTION & HABITAT. Open forest at Pat's Bluff, Lamington National Park, SEQ.

ETYMOLOGY. For Geoff Monteith.

REMARKS. *M. monteithi*, sp. nov. closely resembles a similar large new species of *Misgolas* found throughout southeast Queensland in lower altitudes and onto the lowlands, notably heath.

## DISCUSSION

*Significance of "burnt" brown decorations*. The lateral decorations were noted in *Misgolas robertsi* by Main & Mascord (1974) and (Main, 1985a) in *M. rapax*. Wishart (1992) reported them in *M. hubbardi*, *M. dereki*, *M. kirstiae*, and *M. mascordi*. They are one of the diagnostic characters of females of *A. longipes* but they are widespread but not universal in *Misgolas* (GW). Apart from *A. longipes*, they are here reported also in *A. beaury*, sp. nov. and *A. robertcollinsi*, sp. nov. When present, the dark areas are distinct but interspecifically vary in distribution on the legs (usually I, II and palp), faces (usually both retrolateral and prolateral) and articles (femur, patella, tibia) on which they are present. Also, the height of the decorations relative to the overall height of the lateral face varies. The decorations are less evident in life than in alcohol, at least in *A. longipes*. After an exhaustive examination of Australian idiopids (by RJR) in collections of Australian museums, we can report the decorations are unique to *Arbanitis* and *Misgolas*. Hence, we suggest that the presence of the decorations is phylogenetically informative and may be a synapomorphy of both genera. In species included in *Misgolas* in which they are absent, they may be, of course, secondarily lost. That hypothesis will be tested by other characters.

*Burrow construction behaviour as a synapomorphy*. The use of behavioural characters in araneid systematics has a long history, principally in web type in the Araneoidea (e.g., Scharff & Coddington, 1998). However, except for the many hypotheses of Main (1981), their use in mygalomorphs has been minimal. A notable exception was Raven (1985) who hypothesised that differences—in relative leg strength, leg spination, eye tubercle, caput and rastellum development, and possibly also spinnerets—between the deep basal groups, Fornicephalae and Tuberculotae, were

associated with differences in burrowing habits. The Tuberculotae show little differentiation between the first and fourth legs, a raised eye tubercle, low caput and little rastellum development with weak dorsal spination of legs. In contrast, the Fornicephalae have strongly differentiated legs I and IV, the eye tubercle is low, the caput is high, spines dorsally on the legs III, IV are stronger than ventrally and rastellum development is almost universal.

Main's underlying hypothesis, centred on the Idiopidae, is that burrow structure and associated behaviour is taxonomically and presumably also phylogenetically significant (Main, 1957). In general, burrow construction was considered to correspond with morphological differences between genera. Most notable was the thick plug trapdoor of *Euoplos* (formerly *Arbanitis)* compared with idiopids in which no door is used. A more refined difference lay in the separation of *Cataxia* and *Homogona*, the former builds a half-moon-shaped and often ornate door, whereas in *Homogona*, it is a soft flap—clearly the origin of the door.

In *Arbanitis* and *Misgolas*, four burrow entrance types are known, all lack a door. In the species termed "Tube spiders" (*M. robertsi* and *M. mascordi*), the burrow is significantly extended above the ground, held upright by its attachment to saplings, trunks, roots or rocks. In the *A. longipes* group, the burrow entrance is basically flush with the ground. In *M. rapax* and *M. hubbardi*, the "burrow has a rigid, funnel-like entrance; the lip is always oblique at an angle of between 30° and 80° in the manner of a hood and is disguised and strengthened with attached leaves and other small pieces of vegetation" (Wishart, 1992). In *M. kirstae* Wishart, 1992 and *M. gracilis* (Hogg), the entrances have a soft flap door, as in *Homogona*. The differences do not correlate with either the reduction or absence of a spur on tibia I or the rounded cymbial lobe on the male palp; flush entrance burrow builders occur in both groups. However, the stalked burrow of the Tube spiders may be the synapomorphy of a group.

*Matching conspecific males and females of sympatric congeners in somatically homogeneous groups.* In most spider families, at least two species occur in sympatry but usually matching conspecific males and females presents little problem as they belong to somatically distinct genera. However, many spider genera are diagnosed on characters found only in adult males (e.g., Davies 1998; Platnick, 2000). Sexual dimorphism in spiders is often quite strong affecting not only "primary" sexual characters (e.g., female epigyne and male palp through which sperm is indirectly transferred), but also spinnerets (e.g., Platnick, 1990), cheliceral development (e.g. Forster, 1970), leg spination (e.g., Raven, 1994), and carapace shape (e.g., Grostal, 1995), as well as abdominal scute development (e.g., Platnick, 2000). Strong sexual dimorphism is present in Araneomorphae (e.g., Davies & Raven, 1980) but often not problematic in this context.

In contrast, in the highly somatically homogenous mygalomorphs, problems generated by sexual dimorphism may become quite acute. In hexathelids, Raven (1978) found strong differences in males and females in carapace setation and leg spination (apart from that of the coupling spur on leg I). However, only in one case did a possible problem appear. Two apparently sympatric species of *Paraembolides*, *P. polesoni* (Raven, 1978) and *P. lugubris* (Raven, 1978), were almost identifical in the shape of the bulb and spination of the male palpal tibia but differed strongly in abdominal pattern and foveal bristles. The species later proved to be closely parapatric in adjacent open forest and rainforest at New England National Park, northeastern New South Wales. That case was unusual in that sexual differences were not useful, even between males of different species, but somatic differences were.

Difficulties arise when no habitat difference is known, i.e., species are sympatric in the same forest. One of us found that matching congeneric males and females of four sympatric species in *Misgolas* at Gerringong (Wishart, 1992) presented a challenge. Characters used to match conspecific sympatric males and females (as well as the widely allopatric *Misgolas mascordi*) were spination of retrodorsal metatarsus IV and ventral abdominal pattern. There were also differences in rastella.

The issue herein was somewhat simplified with *Arbanitis longipes* because long term pitfall trapping at several localities yielded males of only *A. longipes* which was taken as evidence that only one species was present. At Rochedale State Forest, a male and female of a second species were also taken but clear differences between them and those of *A. longipes* were evident. However, the related problem arose when attempting to separate females of *A. longipes* from those of the putative sister species *A. robertcollinsi*. Equally, on Lamington Plateau,

although three species (*Misgolas echo*, *M. monteithi*, *M. bithongabel*) are known only from three different localities (Echo Point, Pats Bluff, Mt Bithongabel, respectively), the fourth (*Arbanitis robertcollinsi*) has been found more widely but is not known to be sympatric with the others. The fourth also appears very commonly in pitfall traps.

The use of pitfall trap data to establish what males are in the area is not foolproof because males of arboreal mygalomorph spiders (e.g., *Migas*, *Sason*) do not feature commonly in pitfall traps (QM spider database). However, if males are takcn in pitfall traps (as for all new species herein), then it is likely that females are ground dwelling. However, the corollary—that males most commonly encountered in traps are conspecific with the most commonly seen females—is not equally valid.

Males of *A. robertcollinsi* are amongst the smallest idiopids on Lamington Plateau and the dorsal abdominal pattern is distinct, at least in ethanol. However, the most evident burrows at Binna Burra, Springbrook and O'Reillys are those of a large tube-building female with no evident pattern in life or dcath.

*Populations and differences.* Bond et al. (2001) claimed absence of [quantifiable] morphological difference bctween genetically divergent populations of a Californian cyrtaucheniid, *Aptostichus simus* (Chamberlin 1917). For the estimation of morphological difference they used only females and a number of non-specific morphometric characters and ratios from them, i.e., relative dimensions of carapace, sternum, sigilla, labium, leg I, labial and maxillary cuspules, spines on the rastellum, and patella and tibia III, and cheliceral dentition. No reason was given for the choice of characters, they are simply characters that have been recorded in descriptions of mygalomorph. As we havc shown here in *Arbanitis longipes* and seen also, for example, in Raven (1994), differences in females are not always reflected in that set of characters but are present in characters specific to the genus, e.g., basifemoral thorns, colour pattern. Equally, those smaller differences in females are correlated with strong and quantifiable differences (spination of tibial apophysis, scopula on tarsi) when the male palp is used but Bond et al. (2001) did not use males.

In *Arbanitis longipes*, at least two distinct populations with diagnostic characters in the extent and number of ranks of spines on the RTA of males have been identified. As indicated above (Variability), the type population is readily diagnosable from that at Mt Tamborine (Fig. 4F) by the less numerous spines. However, populations at Beechmont, Beerwah, Bahrs Scrub and Flinton Hill, have fewer spines with very well separated ranks (Fig. 4). Remarkably, the latter morphotype is geographically interspersed between that of the type form. No characters have been found in females to support the differences in males and clearly a much more intensive study is needed.

## Euoplos Rainbow, 1914

*Euoplos* Rainbow, 1914: 217. Type species by monotypy *Euoplos spinnipes* Rainbow, 1914.

*Evoplos*: Bonnet, 1956: 1892. Incorrect emendation followed also by Main (1985a, b).

*Tambouriniana* Rainbow & Pulleine, 1918: 120. Type species by monotypy, *Tambouriniana variabilis* Rainbow & Pulleine, 1918. First synonymised with *Arbanitis* by Main, 1985a.

*Albaniana* Rainbow & Pulleine, 1918: 122. Type species by subsequent designation of Petrunkevitch (1928:63), *Albaniana inornata* Rainbow & Pulleine, 1918. First synonymised with *Arbanitis* by Main, 1985a.

*Bancroftiana* Rainbow & Pulleine, 1918: 127. Type species by monotypy, *Bancroftiana speciosa* Rainbow & Pulleine, 1918. First synonymised with *Arbanitis* by Main, 1985a: 22.

*Armadalia* Rainbow & Pulleine, 1918: 129. Type species by subsequent designation of Petrunkevitch (1928:63), *Armadalia ornata* Rainbow & Pulleine, 1918. First synonymised with *Arbanitis* by Main, 1985a.

DIAGNOSIS. Differs from all other Australian idiopids by the broad carapace with clearly procurved fovea in males (Eastern Australia) and females; males of Western Australian species may have a straight fovea but have retained the unique broad carapace. Males differs from those of *Misgolas* and *Arbanitis* in the broadly keeled embolus.

Four spinncrets. Eye group as wide behind as in front or wider. Rastellum present in females. Sternum posteriorly broad. Tarsi I, II of males ventrally incrassate, pallid and scopulate. Enlarged dorsal abdominal sigilla absent.

TYPE SPECIES. *Euoplos spinnipes* Rainbow, 1914 by monotypy.

SPECIES INCLUDED

*Mygale annulipes* C.L. Koch, 1842 . . . . . TAS
*Arbanitis bairnsdale* Main, 1995 . . . . . VIC
*Arbanitis ballidu* Main, 2000 . . . . . WA
*Arbanitis festivus* Rainbow & Pulleine, 1918 . . . . . WA
*Cantuaria hoggi* Simon, 1908 . . . . . WA
*Albaniana inornata* Rainbow & Pulleine, 1918 . . . . . WA
*Albaniana ornatus* Rainbow & Pulleine, 1918 . . . Qld
*Arbanitis mcmillani* Main, 2000 . . . . . WA

*Albanitis similaris* Rainbow & Pulleine, 1918 . . . . . Qld
*Euoplos spinnipes* Rainbow, 1914 . . . . . Qld
*Aganippe tasmanica* Hickman, 1928. . . . . Tas
*Tambauriniana variabilis* Rainbow & Pulleine, 1918. . . . . Qld, NSW
*Arbanitis victariensis* Main, 1995 . . . . . Vic
*Armadalia zorodes* Rainbow & Pulleine, 1918 . . . . . SA

REMARKS. In E Australia, the fovea of males and females of *Euoplos* are strongly procurved. However, males of Western Australian species herein included in *Euoplos* have a straight fovea (Main, 2000 and pers. obs. RJR); that suggests that *Albaniana* may be validly restored for those species. However, a cladistic hypothesis is required before making such changes and that is beyond the scope of this work.

DISTRIBUTION. Coastal E and SW Australia.

## CLADISTICS

The following taxa were used as ingroup: *Arbanitis longipes*, *A.beaury*, *A.robertcollinsi*, *Misgolas echo*, *M. monteithi*, *M. hubbardi*, *M. dereki*, *Euoplos variabilis*, *E. similaris*, *Homogona pulleinei* Rainbow, *Cataxia spinipectoris* Main, 1974. The theraphosid, *Chaetopelma* and the cyrtaucheniid, *Kiama*, were used as outgroups.

Characters were taken only from males, with the exception of burrow type, which is taken from females where known.

1. Median haematodocha: 0, normal, slit-like; 1, extensive.

2. Bipartite coupling apophysis on tibia 1: 0, present; 1, absent

3. Bipartite coupling apophysis on tibia 1: 0, strong; 1, weak

4. Cymbial lobe: 0, rounded; 1, acute

5. RTA spines: 0, absent; 1, disordered; 2, in distinct curvi-linear ranks

6. Basal mound on RTA: 0, absent; 1, present

7. Spines on male palpal tarsus: 0, present, strong; 1, absent; 2, weak spines.

8. Fovea: 0, straight; 1, recurved; 2, strongly procurved

9. Eye group: 0, about twice as wide as long; 1, as wide as long; 2, about 1.5 times wider than long.

10. Eye group: 0, about as wide in front as behind; 1, clearly wider in front; 2, clearly wider behind.

11. Secondary apophysis: 0, absent; 1, present.

12. Secondary apophysis: 0, a low tear-shaped lobe in profile; 1, long triangular lobe; 2, a broad-based tapering sinuous lobe; 3, long conical and apically hooked.

13. RTA spine length: 0, absent; 1, all or most short, conical; 2, most at least 3-4 times longer than wide.

14. Embolus tip: 0, pointed; 1, flared

15. Carapace shape: 0, long narrow; 1, broad wide.

16. Decorations on legs: 0, absent; 1, weak; 2, strong.

17. Burrow door: 0, absent; 1, thin, wafer-like; 2, thick plug

18. Male, tarsal spines on 1: 0, few to absent; 1, many strong.

19. Carapace colour: 0, yellow brown; 1, dark brown

20. Caput elevation: 0, low; 1, arched.

21. Embolus shaft: 0, tapers for length; 1, with flared portion

All characters were treated as unordered and equally weighted. The use of unordered characters is notionally an acceptance of the Principle of Indifference (Wilkinson, 1992); most characters used here could be ordered although convention has opposed it.

NONA 2.0 (Goloboff, 1997) was used through Winclada 1.00.08 (Nixon, 2002) with the settings mult*1000, with 1000 replications and 25 starting trees per replication. Six equally parsimonious trees were found (length, 42 steps; ci=0.69; ri=0.78) was found in which the five groups were common to all trees: the three *Arbanitis* species are monophyletic and always basal in position; *Homogona* is the sister group of *Cataxia*; the *Euoplos* species are monophyletic; *Misgolas monteithi* and *M. dereki* are consistently the sister group of *M hubbarbi*; and all idiopids except *Arbanitis* form a monophyletic group. The Nelsen consensus tree is given (Fig. 12) (length, 45 steps; ci=0.64; ri=0.73) Differences in the six cladograms lie entirely with the positions of the *Misgolas bithongabel* and *Misgolas echo* and the relationships within the clade of the genera.

*Misgolas* was not monophyletic in any cladogram. Showing monophyly of *Misgolas* is not one of the objects of this analysis. This was only a small group of species representing many known but undescribed in *Misgolas*. In 2004, Raven (unpublished) surveyed morphological diversity of all male mygalomorphs in museum collections in Australia and found that although the idiopids provide a rich diversity of diagnostic

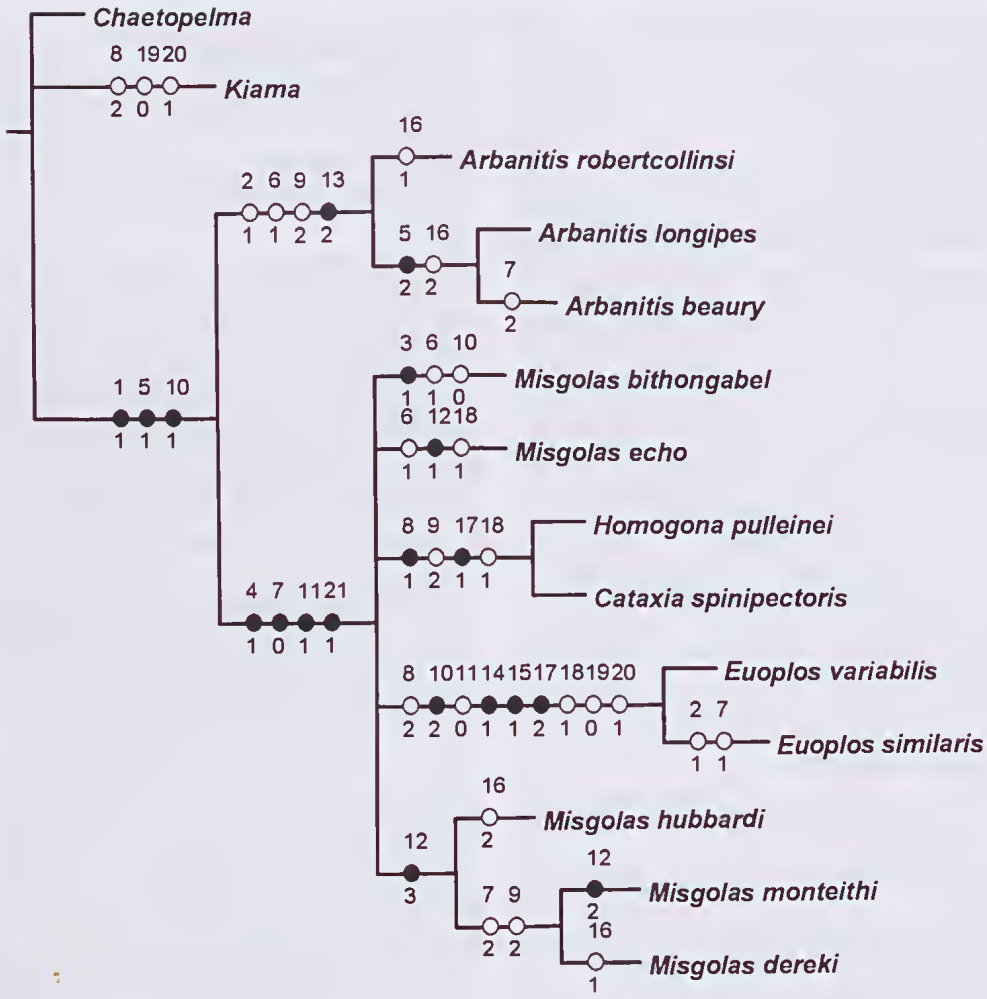


FIG. 12. Cladogram of Nelsen consensus tree; character states marked with solid dots squares are non-homoplasious and unambiguous changes. All unsupported nodes are shown collapsed.

characters, homoplasy is rife in most characters. Hence, numerical phylogenetic analysis of the bigger group will presumably not reflect what has been thought to be natural groups (i.e., genera) and only use of the original Hennigian method will produce a result that is acceptable.

In summary, *Arbanitis* species are rendered monophyletic and are the sister group of the combined genera, *Euoplos, Misgolas, Homogona* and *Cataxia*.

The cladogram places *Arbanitis* as the most plesiomorphic of the Arbanitinae, at least those of eastern Australia. The absence of the pointed cymbial lobe in *Arbanitis*, one synapomorphy of the Idiopidae (Raven, 1985) can either be taken as a homoplasy (i.e., reversal) or as indication that *Arbanitis* should lie basally in the Idiopidae with the pointed cymbial lobe the synapomorphy of all other idiopids. The absence of the male coupling spur in *Arbanitis*, considered by Raven (1985) to be the synapomorphy of the Genysinae + Arbanitinae, implies that *Arbanitis* should be their sister group. (As Main, 1985a had indicated, the tibial spur can be absent within genera, like *Euoplos* among others; that is taken to be a secondary loss.) In that case, the senior family group name for the Australian idiopids is Aganippinae Simon. Until a cladogram including the taxa here used, plus the Gensyinae and

FIG. 13. Distribution of *Arbanitis* (A), and *Misgolas* (B) in southeastern Queensland and northern New South Wales

Idiopinae, supports that hypothesis no change is required.

## BIOGEOGRAPHY

The distribution of *Arbanitis* reported here is from the MacPherson-Macleay overlap and adjacent lowland areas including forests around Brisbane, Moreton Island and Beerwah heath with an outlier west in the Great Dividing Range in northern New South Wales. The cladogram shows *A. robertcollinsi*, from the Lamington Plateau, to be the sister group of all other species and hence the most plesiomorphic species in the genus. Hence, both *A. longipes* and *A. beaury* may have diverged at least by the Eocene as the rainforest contracted to the mountain tops.

The cladogram also implies that that Lamington Plateau is home to the most plesiomorphic genus, *Arbanitis*, in the Idiopidae. That may, at first, seem incongruous; such plesiomorphic taxa are usually found first in Tasmania and New Zealand. However, one of the localities in the distribution of *Arbanitis* — Lamington National Park—is one of the last surviving locations of *Nothofagus* in Australia. In any case, a number of plesiomorphic spider groups occur in sympatry with *Arbanitis robertcollinsi*: the four-lunged araneomorph family Gradungulidae is found in rainforests in the region, along with relict parts of eastern Australia (Forster et al., 1987). Raven (1995) found that the most plesiomorphic state, viz. outlets on legs I, II and IV, of the coxal glands in any known chelicerate occurs in the hexathelid *Bymainiella terraereginae* (Raven, 1976) from the same plateau.

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We are very grateful to Dr Gisela Rack, retired curator and current curator Dr H. Dastysch, Zoologishes Museum, Hamburg (ZMH), for their thoroughness in addressing the unresolved Goddefroy collection and providing a loan of the rediscovered holotype and subsequent warm and refreshing hospitality. Drs Mark Harvey, Western Australian Museum (WAM), and Barbara York Main provided comment, hospitality and challenging discussion which improved the scholarship of this work. Mr John Murphy also provided welcome hospitality during RJR's visit to Europe. Drs Marshall Hedin, Jason Bond, David Rowell, and Jessica Worthington-Wilmer provided encouragement, comment and support on molecular issues. Some data used herein were gathered with Australian Research Grant support to RJR. Graham Milledge, Australian Museum (AMS), Sydney and David Hirst, South Australian Museum (SAM), Adelaide, both provided expeditious loans and valued access to the respective collections in their care. Dr Barbara Baehr, Queensland Museum (QM), patiently provided valued counter-point, discussion and support throughout the life of the manuscript.

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## APPENDIX

Data matrix for cladistic analysis. Character 0 is deactivated.

| TAXON | CHARACTER STATES |
|---|---|
| *Chaetopelma* | 000000 -1000 0—00 000100 |
| *Kiania* | 00—00 -1200 0—00 000010 |
| *Euoplos variabilis* | 010011 00202 0-111 021011 |
| *Homogona pulleinei* | 010011 00121 10100 011101 |
| *Arbanitis longipes* | 011-02 11021 0-200 200100 |
| *Arbanitis robertcollinsi* | 011-01 11021 0-200 100100 |
| *Arbanitis beaury* | 011-02 12021 0-200 200100 |
| *Misgolas monteithi* | 010011 02021 12100 000101 |
| *Misgolas bithongabel* | 010111 10000 10100 0?0101 |
| *Misgolas hubbardi* | 010011 00001 13100 200101 |
| *Misgolas dereki* | 010011 02021 13100 100101 |
| *Misgolas echo* | 010011 10001 11100 0?1101 |
| *Euoplos similaris* | 011-11 01202 0-111 021011 |
| *Cataxia spinipectoris* | 010011 00121 10100 011101 |

**A NEW SAWFLY FROM THE TRIASSIC OF QUEENSLAND (HYMENOPTERA: XYELIDAE).** *Memoirs of the Queensland Museum 51(2): 558. 2005:*—The earliest records of the Hymenoptera are a handful of Late Triassic sawflies from Central Asia, South Africa, and Australia (Riek, 1955; Rasnitsyn, 1964, 1969; Schlüter, 2000). These species belong to the basal Xyelidae (Archihymenoptera *sensu* Grimaldi & Engel, 2005). The first of these early xyelids to be discovered were two specimens from the Late Triassic Mt. Crosby Formation near Ipswich, Queensland for which Riek (1955) proposed *Archexyela* to accommodate *A.. crosbyi*. Herein I provide the description of a second species (based on a third specimen: Fig. 1) of *Archexyela* from the same formation. The new species exhibits a number of significant differences from the type species but is placed in the same genus based on the shared combination of pterostigma sclerotized only at extreme base, otherwise membranous; 1r-rs meeting base of pterostigma; 2r-rs meeting Rs1 (rather than stem of Rs); Sc free to base of wing.

Family XYELIDAE Newman, 1835

**Archexyela ipswichensis** sp. nov. (Figs 1–2)

*Archexyela* sp., Jell, 2004: 106.

*Archexyela* sp., Grimaldi & Engel, 2005: 410.

*Diagnosis*. The new species can be distinguished from *A. crosbyi* by the evanescent vein (sclerotized only at its base) basad Sc-R loop (Fig. 2); Sc and R running alongside each other from base and briefly arching apart (to form small subcostal cell: here termed the Sc-R loop) before termination of Sc into Rs just before separation of Rs; second free abscissa of Rs nearly twice as long as 1r-rs (approximately equal in length in *A. crosbyi*); 2r-rs about as long as first free abscissa of Rs1 (2r-rs nearly twice as long as first free abscissa Rs1 in *A. crosbyi*); first free abscissa of Cu distinctly arched anteriorly; and first medial cell elongate.

*Description*. Forewing 10 mm long (as preserved); Sc free from base to slightly more than half distance to pterostigmal base, running abruptly alongside R (i.e., without subcostal cell between veins for most of their length), terminating into R just basad Rs separation; Rs arching posteriorly slightly before Sc termination to form a small subcostal cell for a short length (here termed the Sc-R loop: Fig. 2). Rs separating slightly distad termination of Sc into R and well proximad pterostigmal base (Fig. 2); first free abscissa of Rs only slightly angled toward wing apex; second free abscissa of Rs nearly twice as long as 1r-rs; 1r-rs meeting base of pterostigma; third free abscissa of Rs strongly arched posteriorly; 2r-rs meeting Rs1, about as long as first free abscissa of Rs1; M+Cu weakly arching anteriorly proximad separation of Cu; first free abscissa of M nearly twice as long as first free abscissa of Rs; Cu separating from M+Cu proximad level of Sc termination; Cu arching gently posteriorly; first medial cell elongate; 1cu-a relatively long, nearly three-quarters length second free abscissa Cu; 1A straight; crossvein a elongate, oblique; 2A+3A with typical proximal arch. Pterostigma elongate, narrowed (about as wide as costal cell), only sclerotized at extreme base, otherwise membranous (similar to *A. crosbyi*, *Asioxyela smilodon* Rasnitsyn, 1964, as well as various Cretaceous genera).

*Holotype*. Queensland Museum Fossil Collection 44154 (Fig. 1), Late Triassic, Carnian. Mt. Crosby Formation, Ipswich Coal Measures, from North of Ipswich, Queensland, Australia.

*Etymology*. From near Ipswich.

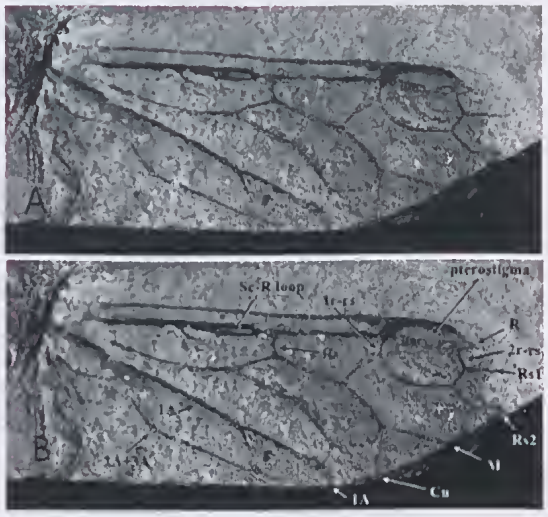


Fig. 1. Holotype of *Archexyela ipswichensis* sp. nov. (QMF44154). A. Forewing as preserved. B. Forewing with labels for particular venational elements overlaid.

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# A NEW SPECIES OF SCINCID LIZARD, *SAPROSCINCUS EUNGELLENSIS*, FROM MID-EASTERN QUEENSLAND

ROSS A. SADLIER, PATRICK J. COUPER, DONALD J. COLGAN, ERIC VANDERDUYS & EDWINA RICKARD

Sadlier, R.A., Couper, P.J., Colgan, D.J., Vanderduys, E. & Rickard, E. 2005 12 31: A new species of scincid lizard, *Saproscincus eungellensis*, from mid-eastern Queensland. Memoirs of the Queensland Museum **51**(2): 559-571. Brisbane. ISSN 0079-8835.

A skink, *Saproscincus eungellensis* sp. nov., is described from high altitude (>700 m) rainforests on the Clarke Range (21°01'S, 148°36'S) in mid-eastern Queensland. It is most similar in morphology, behavior, and habitat preference to several species (*S. challengeri*, *S. spectabilis*, and *S. rosei* - the '*challengeri*' group) from the moist forests of northeastern New South Wales and southeastern Queensland, approximately 800km or more to the south, and in appearance most closely resembles *S. challengeri*, a species restricted to the Border Ranges region. Its large size, differences in scalation, and genetic data, readily distinguish *S. eungellensis* sp. nov. from these species. Genetic data from two independent mitochondrial DNA studies support the close relationship of *Saproscincus eungellensis* sp. nov. with the southern taxa, but give different interpretations of intraspecific relationships between these species. The combined 12S ribosomal RNA and Cytochrome *b* data presented here clearly identifies *Saproscincus eungellensis* sp. nov. as a member of the '*challengeri*' group, and to a lesser degree as basal to the other species in the group. The description of this species brings the number of reptiles endemic to the Mackay Coast to eight (*Phyllurus championae, P. isis, P. nepthys, P. ossa, Eulamprus amplus, E. luteilateralis, Saproscincus eungellensis* sp. nov. and *S. hannahae*). Of these, *P. nepthys, E. luteilateralis* and *S. eungellensis* sp. nov. are confined to the Clarke Range. Because of its narrowly-restricted distribution (< 500km$^2$) and its reliance upon high altitude rainforests, *S. eungellensis* sp. nov faces a projected decline in its area of occupancy through processes relating to global warming and interactions from other threatening processes. It satisfies the criteria for an Endangered listing under the Queensland Nature Conservation Act 1992, Nature Conservation (Wildlife) Regulation 1994. ☐ Saproscincus eungellensis, *new species*, *Scincidae, rainforests, Queensland.*

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Research into the lizards in eastern Australian rainforests, in particular the gekkonids *Saltuarius* and *Phyllurus* and the scincid *Saproscincus*, has led to discovery of several new species in the past decade. Some of these are the result of recent field collections made in areas not before adequately investigated (Couper et al., 2000; Hoskin et al., 2003), the recognition of distinct sibling taxa from museum based collections (Couper & Keim, 1998), or a combination of the two (Couper et al., 1993).

In the 1970's a series of surveys of major rainforest blocks in Queensland and areas of northern NSW (Broadbent & Clark, 1976) investigated several sites in mid-eastern Queensland including the high elevation forests of Eungella (20°55'S, 148°30'E) in the Clarke Range west of Mackay. Voucher collections were lodged in the Australian and Queensland Museums. Amongst this material were two specimens of a moderate-sized skink assignable to *Saproscincus*, but not readily allocated to any existing species.

Acquisition of additional specimens allows assessment of morphological variation within the new taxon and variation between it and other species of *Saproscincus*. Tissue samples obtained from these specimens have facilitated comparative intrageneric genetic studies that provide an independent assessment of the status of the species. The results of these studies identify the large *Saproscincus* from the Eungella area as a new species, whose closest relatives are a lineage of three species, the '*challengeri*' group (*S. challengeri*, *S. spectabilis*, and *S. rosei*) from SE Qld and NE NSW.

## MATERIALS AND METHODS

Abbreviations: QM=Queensland Museum, Brisbane; AMS=Australian Museum, Sydney.

The following suite of morphological characters were scored for each specimen where possible: snout to vent length (SVL) - measured from tip of snout to caudal edge of anal scales; axilla to groin distance - measured from middle of base of forelimb to base of hindlimb; forelimb to snout length - measured from tip of snout to middle of base of forelimb; hindlimb length - measured from middle of base of hindlimb to tip of fourth toe including claw; tail length - measured from caudal edge of anal scales to tip of tail, the degree to which the original tail is present being determined by X-ray. Body measurements (axilla to groin, forelimb to snout, hindlimb) are for adult specimens, and are expressed as percentages of snout to vent length in the species accounts. Specimens were regarded as sexually mature (adults) if they showed signs of reproductive maturity (presence of enlarged yolked ovarian follicles or eggs in females, and presence of enlarged testes and distinctive colouration in males) and/or if they were within the size class as determined by the minimum size at reproductive maturity.

Head scalation generally follows Taylor (1935). Midbody scale rows - number of longitudinal scale rows around body counted midway between axilla and groin. Paravertebral scales - number of scales in a paravertebral row from first scale posterior of parietal scale to last scale at the level of vent opening. Fourth finger and toe scales - number of dorsal scales on fourth digit of hand and foot, distal scale contains claw, basal scale of fourth finger is usually present as a single large scale common to the base of the fourth finger, and basal scale of fourth toe broadly contacts basal scale of adjacent third toe. Fourth finger and toe lamellae - number of ventral scales on fourth digit of hand and foot, distal scale contains claw and basal scale is the most proximal largely undivided scale at a point level with intersection of third and fourth digits. Bilateral scalation characters were scored on both sides. Individual values determined the range and were used in determining percentage frequencies. The mean value of the two individual vales was used in determining the overall mean value for each species, and deviation from the mean value is standard deviation.

Phalangeal formula and the number of presacral and postsacral vertebrae was assessed by X-ray.

DNA EXTRACTION AND SEQUENCING. Specimens used and the corresponding registration numbers are listed in Appendix. DNA was extracted from a small amount of tissue (30–50mg) by the CTAB method of Saghai-Maroof et al. (1984) or the AMRESCO RapidGene™ Genomic DNA Purification Kit according to manufacturer's instructions. The DNA was resuspended in 100-200µl of TE buffer (depending on pellet size) and 3µl of this preparation was run on a 1% agarose gel containing ethidium bromide and UV-visualised. Where the DNA was low in abundance it was used undiluted. Otherwise, the DNA was diluted between 1 in 10 and 1 in 40 with water before use.

The primer pairs used and segment abbreviations used herein are as follows, with ambiguities written in standard IUB codes:

Cytochrome *b* (Cytb) was generally amplified using the Kocher et al. (1989) 'universal' primers):

CytbF: 5'-AAA AAG CTT CCA TCC AAC ATC TCA GCA TGA TGA AA-3' and

CytbR: 5'-AAA CTG CAG CCC CTC AGA ATG ATA TTT GTC CTC A-3'

Specimens that could not be amplified with this pair were amplified with the primers:

Cytb(skink)F: 5'-TGC CTC ATC ATW CAA GTA CTY AC-3'

Cytb(skink)R: 5'- GTG AGG GTG GCR TTR TCT ACT G-3'

These were designed for this study.

12S ribosomal DNA (12S) was also amplified using primers designed by Kocher et al. (1989):

12SF (= L1091): 5'-AAA AAG CTT CAA ACT GGG ATT AGA TAC CCC-3'

12SR (=H1478): 5'-TGA CTG CAG AGG GTG ACG GGC GGT GTG T-3'

PCR was performed using 1.0 Units of QIAGEN (Venlo, The Netherlands) thermostable DNA polymerase, in the manufacturer's buffer (1X concentration), 0.05 mM dNTPs, 3.5 mM $MgCl_2$ and 12.5 pmol of each primer in a total reaction made up to a volume of 49µl with water. 1µL of diluted DNA was added. Negative controls (without DNA) were included in each reaction array. To optimise PCR products, annealing temperatures and times, and $MgCl_2$ concentration were varied. For Cytb and

CytB-skink primer pairs, the cycling profile was as follows: (95°C for 5 min, 50°C for1 min, 72°C for 1 min) for one cycle, (95°C for 30 sec, 50°C for 1 min, 72°C for 1 min) for 32 cycles and 72°C for 3 min for the final cycle. A similar profile was conducted for 12S except that the annealing temperature was increased to 52°C. Reaction products were resolved on 2% agarose gels. All single band products were purified using AMPURE magnetic beads (Agencourt) processed by a liquid handling system (Corbett Engineering CAS-3800).

Products were sequenced in both directions on an Applied Biosystems (ABI)® 310 DNA Sequencer using the DyeDeoxy™ Terminator sequencing method according to the manufacturer's protocol except that reactions were scaled down to 10µl using 2µl Big Dye version 2.0 reaction mix (Applied Biosystems) Sequencing reactions were purified using CleanSeq magnetic beads (Agencourt) on the Corbett liquid handler.

SEQUENCE ALIGNMENT AND PHYLOGENETIC ANALYSIS. Consensus sequences for each taxon were generated by assembling forward and reverse sequences using Sequencher (Gene Codes). Sequences were aligned using default values for parameters in CLUSTAL X (Thompson et al., 1994). There were no areas of uncertain alignment in either of the genes.

Average genetic distances between groups of sequences were determined by MEGA 3.1 (Kumar et al., 2004). Values for the Kimura two-parameter metric are reported here.

Maximum parsimony analyses were carried out for each data set separately and in combination, using PAUP* 4.0. version b10 (Swofford, 2001) with heuristic searches for unweighted analysis of the genes either singly or combined (200 replications of random stepwise addition of taxa were conducted with no more than 200 trees greater than length 300 kept in each replicate). Analyses were performed using the tree-bisection-reconnection (TBR) branch-swapping algorithm. MULPARS was in effect. The steepest descent option was not enforced and accelerated transformation for character optimisation was assumed. Zero length branches were collapsed to give polytomies. Gaps were treated as unknown in all analyses.

For maximum likelihood analyses, the GTR+I+G model was assumed with the following settings determined by the Akaike Information Criterion as implemented in MODELTEST (Posada and Crandall, 1998). The number of substitution types was six, with substitution rate-matrix parameters estimated as (A to C: 19299.9316, A to G: 123654.4922; A to T: 21759.3789; C to G: 10480.1836; C to T: 203837.5469; and G to T: 1.0000). The assumed nucleotide frequencies were (A: 0.3206 C: 0.2823 G: 0.1775 T: 0.2196). To accommodate among-site rate variation the proportion of invariable sites was estimated as 0.5269 and the distribution of rates at variable sites assumed to follow the gamma distribution with $\alpha = 0.8790$ with the number of rate categories set at four. Other parameters took the default values in PAUP 4.0.

Bayesian analyses were conducted using MrBayes (Version 3.01) (Huelsenbeck & Ronquist, 2001). Markov Chains were run for 400,000 steps and the first 60,000 were discarded (after examination of topology probabilities) to allow for convergence. Four differentially heated chains were run simultaneously. Topologies were sampled every 100 generations. Likelihood settings were determined during the run. These were: (i) base frequencies; (ii) the independent rates of the six substitution types; (iii) the proportion of invariable sites; and (iv) the shape parameter of the gamma distribution that was assumed for variation in the rate of substitution between nucleotide positions in the alignment. Parameter estimation was conducted separately for each gene (and each codon position within coding sequences) using a character partition and the "unlink" command in MrBayes.

The 12S rDNA dataset comprised 52 sequences from *Saproscincus* plus five outgroup sequences from the skinks *Lampropholis* (2), *Harrisoniascincus* (1), and *Carlia* (2). These outgroup genera are all members of the '*Pseudemoia*' group (as defined by Greer, 1989). *Lampropholis* was identified by Greer (1989) as the closest living relative to *Saproscincus*, and these two genera along with *Carlia* (and *Lygisaurus*) form a subgroup that shares a unique derived character state of the hemipenis - *Harrisoniascincus* was chosen as a distant representative that lies outside this subgroup. In the alignment of 393 bases, 277 were invariant, 7 were variable but parsimony uninformative, and 109 were informative. The Cytb dataset comprised 40 sequences from *Saproscincus* plus outgroup sequences from the genus *Lampropholis* (2), *Harrisoniascincus* (1), and

TABLE 1. Comparison of size and key scalation characters between members of the *Saproscincus* '*challengeri*' group - comparative data for *S. challengeri*, *S. spectabilis* and *S. rosei* from Sadlier et al., 1993.

| | *Saproscincus eungellensis* | *Saproscincus challengeri* | *Saproscincus spectabilis* | *Saproscincus rosei* |
|---|---|---|---|---|
| Adult body length<br>maximum SVL | 67 | 57 | 59 | 64 |
| Midbody scale rows<br>range<br>mean±sd.<br>N | 22-24<br>23.3 ± 0.95<br>13 | 23-26<br>24.6 ± 1.9<br>63 | 22-24<br>22.7 ± 0.9<br>58 | 22-26<br>24.1 ± 0.9<br>101 |
| paravertebral scale rows<br>range<br>mean±sd.<br>N | 55-58<br>57.0 ± 1.0<br>13 | 54-63<br>57.6 ± 1.6<br>63 | 56-61<br>57.7 ± 1.7<br>58 | 55-67<br>58.8 ± 2.2<br>101 |
| fourth finger scales<br>range<br>mean±sd.<br>N | 9-12<br>10.7 ± 0.5<br>13 | 9-11<br>10.0 ± 0.3<br>63 | 9-11<br>10.2 ± 0.4<br>57 | 8-11<br>9.7 ± 0.8<br>100 |
| fourth finger lamellae<br>range<br>mean±sd.<br>N | 18-24<br>20.3 ± 1.45<br>13 | 15-19<br>17.3 ± 0.9<br>63 | 16-21<br>17.9 ± 1.0<br>57 | 14-18<br>15.3 ± 0.9<br>100 |
| fourth toe scales<br>range<br>mean±sd.<br>N | 10-14<br>11.8 ± 0.8<br>13 | 10-13<br>11.2 ± 0.4<br>63 | 11-14<br>12.3 ± 0.9<br>58 | 10-14<br>11.2 ± 0.6<br>100 |
| fourth toe lamellae<br>range<br>mean±sd.<br>N | 26-34<br>28.5 ± 2.2<br>13 | 23-27<br>24.3 ± 1.0<br>63 | 22-28<br>24.8 ± 1.4<br>58 | 17-24<br>21.0 ± 1.2<br>100 |

*Carlia* (2). In the alignment of 381 bases, 214 were invariant, 11 were variable but parsimony uninformative, and 156 informative.

## SYSTEMATICS

### Saproscincus Wells & Wellington, 1984

*Saproscincus* is a group of eleven species of moderately small to very small scincid lizards occurring along the tropical to temperate east coast of Australia. Greer (1989) diagnosed *Saproscincus* from its nearest living relative, *Lampropholis*, on the basis of a reduced number of labial scales (six *vs* seven) and in having a pale spot at the base of thigh. Within the genus a monophyletic group of species restricted to rainforest habitats of mid E and NE Queensland has been identified (Greer & Kluge, 1980; Greer 1989), that now comprises *S. basiliscus*; *S. tetradactyla*; *S. czechurai*; *S. hannahae* and *S. lewisi*. The remaining members of the genus fall into one of two smaller morphological groups based largely on overall similarity. The '*challengeri*' group (*S. challengeri*, *S. spectabilis*, and *S. rosei* - Sadlier et al., 1993) from moist closed forest habitats from mid E NSW to SE Queensland, and the '*mustelinus*' group, which consists of two species, *S. mustelinus* from Victoria to the N NSW highlands, and *S. oriaris* from near coastal habitats of the mid N NSW coast to the sand islands of SEQ (North Stradbroke Island, photographic record, Wildnet, EPA).

*Saproscincus eungellensis* sp. nov. is most similar in morphology to the species in the '*challengeri*' group. Its exceptionally large size in combination with a suite of scalation characters (see diagnoses below and Table 1) indicate it is not conspecific with any other member of the genus. This assessment of both its distinctiveness and immediate relationships is supported by the molecular data presented here and by Moussalli et al. (2005).

### Saproscincus eungellensis sp. nov. (Figs 1-3)

MATERIAL EXAMINED. HOLOTYPE: QMJ76811 upper Finch Hatton Creek (21°09'S 148°38'E), 28 Nov., 2001. PARATYPES: QMJ49668 Eungella N.P. (20°55'S 148°30'E); QMJ76810 upper Finch Hatton Creek (21°09'S 148°38'E); QMJ76812 upper St Helen's Creek catchment (20°54'S 148°47'E); QMJ76813 upper Finch Hatton Creek (21°09'S 148°38'E); QMJ76814 Mt Dalrymple road near Clarke Range (21°02'S 148°38'E); QMJ79934 Mt William

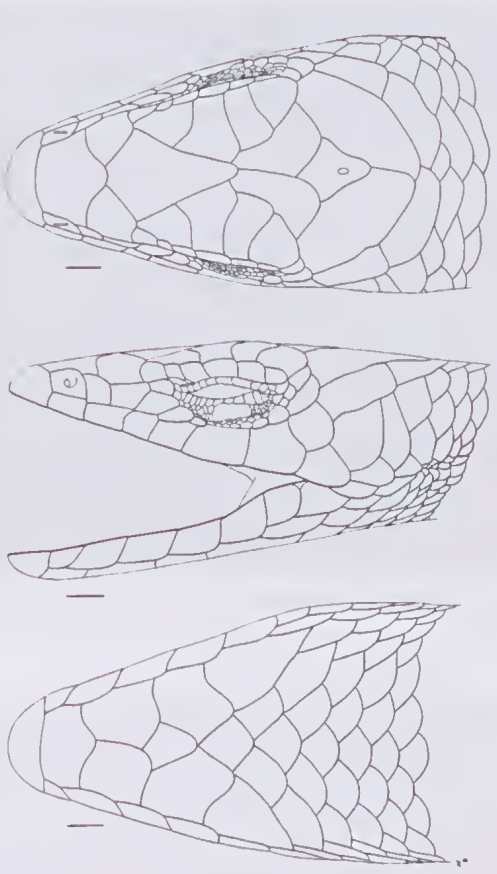

FIG. 1. Dorsal (upper), lateral (middle), and ventral (lower) views of the headshields of the holotype of *Saproscincus eungellensis* sp. nov. This specimen is atypical in having seven rather than six upper labial scales).

(21°01'40"S 148°36'15"E); QMJ78473-77 headwaters of Cattle Creek, Mt William (21°01'48"S 148°36'36"E); AMSR47495-96 Mt William via Eungella (21°01'S 148°36'E).

DIAGNOSIS. Frontoparietal scales paired and distinct from interparietal; upper labial scales six, with the fourth located under the eye; body scales smooth; limbs pentadactyl; and a dark-edged, pale spot at the base of thigh; parietal scales each bordered by a single nuchal and temporal scale; lamellae beneath the fourth toe 26-34; supraciliary scales usually six. The first five characters will identify the species described here as a member of *Saproscincus*. The sixth character will distinguish it from *S. basiliscus*; *S. tetradactyla*; *S. czechurai*; *S. hannahae* and *S. lewisi*, all of which a single nuchal and two temporal scales bordering each parietal scale The high number of lamellae beneath the fourth toe and modal number of supraciliary scales in combination will usually serve in distinguishing *S. eungellensis* from the other members of the '*challengeri*' species group (see Table 1), however no single scalation character will serve to unequivocally identify the new species from the other members of '*challengeri*' species group.

*Saproscincus eungellensis* is most similar to *S. challengeri* in having a modal number of six supraciliary scales, but differs in being markedly larger in adult body size for both sexes, and in having significantly more lamellae beneath the fourth toe. Sexual dimorphism in adult body colouration is more prevalent in *S. eungellensis* with the majority of adult females (70%) having a uniformly coloured unmarked dorsal surface, whereas this pattern of sexual dimorphism occurs in much lower frequencies (<20%) in *S. challengeri* (Sadlier et al., 1993).

In addition to these colour and scalation differences, the distinctiveness of the new taxon is strongly supported by DNA sequence data. Direct comparison between five individuals of *S. eungellensis* and four individuals (two each from two localities) of *S. challengeri* for the mitochondrial 12S gene shows a high level of sequence divergence between these putative species (average Kimura pairwise distances between the groups is 0.128), and no or very low levels of divergence within each population (no haplotype variation being observed in the specimens scored from either species). This level of genetic differentiation suggests the two widely allopatric populations represent two distinct evolutionary lineages.

ETYMOLOGY. From Eungella.

DESCRIPTION. Based on the type series of 14 specimens (38.0-67.0mm SVL), comprising 5 adult males, 7 adult females, 1 subadult, and 1 juvenile.

*Measurements* (based on adults only): maximum SVL of ♂♂ 58.0mm, ♀♀ 67.0mm; distance from axilla to groin 53.3-58.5% of SVL (= 56.4%, n = 12); hindlimb length 35.1-41.9% of SVL (= 38.1%, n=12); tail length 145.6% of SVL for adult QMJ76812 with most complete tail.

*Scalation* (based on adults and one subadult): prefrontals moderately large and usually

FIG. 2. *Saproscincus eungellensis* sp. nov., QMJ78612, an adult female from upper St Helens Creek –dorsal surface with scattered pale and dark markings.

moderately separated (77%), occasionally more narrowly seperated; frontoparietals paired; interparietal distinct; parietals each bordered by a single large upper secondary temporal and a pair of transversely enlarged nuchal scales, the latter occasionally separated from contacting medially (31%); nasals widely separated; loreals two; supraciliaries usually 6 (88.5%), rarely 5 (7.5%) or 7; upper labials usually 6 (81%), sometimes 7; primary temporal single; lower secondary temporal single; tertiary temporals usually single (77%), occasionally two; postlabials two; lower eyelid with an obvious, centrally located semi-transparent disc, and contacting the subocular supralabial.

Midbody scale rows 22-24 ( = 23.3 ± 0.95, n = 13); paravertebral scales 55-58 ( = 57.0 ± 1.00, n = 13) – no sexual dimorphism between 5 males and 7 females ( 56.2 *vs* 57.4, $t_{10}$ = -2.600, P<-0.027); scales on top of fourth finger 9-12 ( = 10.7 ± 0.52, n = 13); lamellae beneath fourth finger 18-24 ( = 20.3 ± 1.45, n = 13); scales on top of fourth toe 10-14 ( = 11.8 ± 0.78, n = 13); lamellae beneath fourth toe 26-34 ( = 28.4 ± 2.20, n = 13).

*Osteology*: presacral vertebrae 27 (n = 11) – 28 (n =1); postsacral vertebrae 51 (QMJ79934 – juvenile specimen with complete tail with vertebrae extending to the tip); phalangeal formula for manus and pes 2.3.4.5.3 and 2.3.4.5.4 respectively.

*Coloration:* Adult males – dorsal surface of body and limbs mid brown with scattered paler markings (usually a single whole scale) and less frequently with finer dark flecks, the lateral surface usually becoming lighter on the side of the head and neck and towards the ventral surface. Head mid brown above (similar to body) and variably with a concentration of fine dark brown markings around the posterior edge of the parietal and frontoparictal scales. Junction of lateral and dorsal surface defined by a series of dark markings on scale row three, continuous anteriorly with a broad dark temporal streak that extends from the level of the ear opening to the nasal. Dark upper lateral markings on the body form a near continuous line along the third or fourth scale row. Ventral surface pale with fine dark brown flecks on the neck, body, and tail and either distributed evenly and forming regular (but broken) longitudinal rows over most of the body; or only as regular rows on the outer edges of the venter with sparse scattered markings centrally; or only as scattered flecks. Tail with dark brown markings along the ventrolateral margin.

Adult females – two colour forms are present, one is similar to adult males (but darker) in having scattered pale and dark markings on the dorsal surface (Fig. 2), and is represented by two adults (J76812 & J76814). The more common form has a uniform light or mid-brown dorsal

FIG. 3. *Saproscincus eungellensis* sp. nov., QMJ78610, an adult female from upper Finch Hatton Creek – uniform dorsal surface.

surface with no markings (Fig. 3), and gives the body a distinctive two-toned appearance. Lateral surface brown to grey (lighter than dorsum), defined by a dark brown dorsolateral stripe (along scale rows three and four), that is continuous with a dark temporal streak. Dark dorsolateral stripe pale edged above (1/2 scale width) that broadens significantly into a broader band (1-1.5 scales width) just posterior of the hindlimbs. Markings on underside of body and tail as in males.

Subadult and juvenile - colour pattern typical of adult males.

REPRODUCTION: Two ♀♀ (QMJ76810, QMJ76811) collected at the very end of the dry season in late November 2003 each had six shelled oviducal eggs, two other adult females (QMJ76812, QMJ76814) collected at this time had large convoluted oviducts indicating that egg-laying had already taken place in these individuals.

COMPARISON. *Saproscincus eungellensis* is readily distinguished from the 'northern' lineage (*S. basiliscus*; *S. tetradactyla*; *S. czechurai*; *S. hannahae*; and *S. lewisi*) by its much larger size (max. SVL of 49.8mm for *S. basiliscus*, largest member of the group, and 42.3mm for regionally sympatric *S. hannahae* - Couper & Keim, 1998) and in having the parietal scales each bordered by a single enlarged nuchal scale and upper secondary temporal scale (*vs* a nuchal and two upper temporal scales).

It can be distinguished from the '*mustelinus*' group (*S. mustelinus* and *S. oriaris)* in having more lamellae beneath the fourth finger (18-24 *vs* 9-14 and 13-16 respectively) and more lamellae beneath the fourth toe (26-34 *vs* 14-19 and 18-22 respectively (Sadlier, 1998, table 1).

No single scalation character will unequivocally differentiate *S. eungellensis* from the '*challengeri*' species group. The high number of lamellae beneath the fourth toe in *S. eungellensis* (26-34) is non-overlapping with *S. rosei* (17-24), almost so with *S. challengeri* (22-27), and to a lesser extent with *S. spectabilis* (22-28). Most *S. eungellensis* and *S. challengeri* have six supraciliary scales whereas *S. rosei* and *S. spectabilis* usually have seven. The large size of *S. eungellensis* will assist in distinguishing its mature individuals. Adult female *S. eungellensis* reach a maximum SVL of 67 mm (Table 1) which is 10mm longer than the largest *S. challengeri*, 8mm longer than the largest *S. galli*, and 3mm longer than the largest *S. rosei* recorded by Sadlier et al. (1993).

DISTRIBUTION AND HABITAT. *S. eungellensis* is known from five locations, all above 700 m, in the Clarke Range, mid E Queensland (Fig. 4).

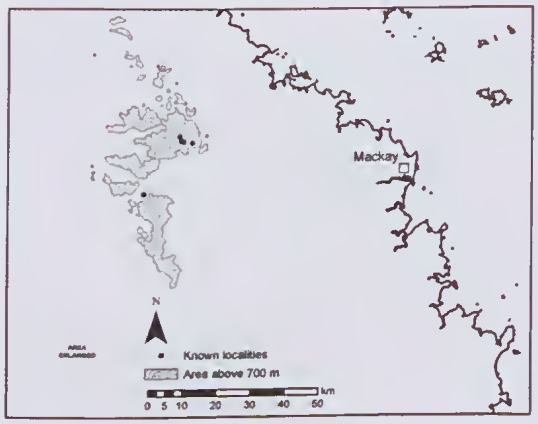


FIG. 4. Distribution map for *Saproscincus eungellensis* sp. nov. Black dots are known sites.

The upper Fineh Hatton Creek (QMJ76810-11, QMJ76813), upper St Helen's Creek (QMJ76812), and Mt. Dalrymple road (QMJ76814) speeimens were eollected from thiek rainforest in elose proximity to rainforest streams (<10 m) (Figs 5, 6). Vegetation included Water Fern (*Bleehnum cartilagineum*) and Silky Fan Fern (*Stieherus flabellatus*), both of whieh oeeur along roeky seetions of the ereek line. Alexander and/or Pieeabeen palms (*Arehontophoenix alexandrae* and *A. eunninghamiana*, respeetively) were present and the eanopy gap above the ereek was eriss-erossed with oeeasional lianas and lawyer eanes (*Calamus* sp.). In several eases the skinks were within the splash zone of riffles and waterfalls. These were often wet, either from splashing or direet immersion. They appeared to be eool and apparently had some diffieulty moving. Individuals would often allow a elose approaeh without fleeing. A single individual was seen, but not eolleeted, at the Broken River eampground (1210'10"S, 148° 30'17"E). It was among introduced, unmown lawn grasses where sunlight broke through the riparian trees. It was within 20m of a large pool. *Eulamprus amplus*, *E. luteilateralis*, and *Saproscincus hannahae* were observed in sympatry with *S. eungellensis* (habitat observations, E.V.).

CONSERVATION STATUS. Using the 'Nomination form and guidelines for listing proteeted wildlife under the *Nature Conservation Act 1992*' (Environmental Proteetion Ageney, Queensland Parks and Wildlife Serviee), *S. eungellensis* qualifies as an Endangered speeies (B2). It meets the following seleetion eriteria: 1) 'Area of oeeupaney estimated to be less than 500 km$^2$'; 2) 'known to exist at no more than five loeations'; 3) 'Continuing deeline...projeeted, in...area, extent and/or quality of habitat'.

The maximum area of oeeupaney was ealeulated using AreMap 8 (ESRI GIS and Mapping Software) eombined with 2002 satellite imagery (E.V.). 'Islands' of suitable habitat, above 700m, were ineluded in the ealeulation only if the long axis was greater than 1km. Using this approaeh, a total area of 498km$^2$ is available, but this eontains 39km$^2$ of eleared land and 3.5km$^2$ of drier woodlands (visible in the satellite imagery). Henee, the area of suitable habitat is approximately 459km$^2$. If *S. eungellensis* is restrieted to ereek lines, as eolleetion data and observational reeords suggest, its true distribution is eonsiderably less.

*Saproscincus eungellensis* is known from five loeations: Upper Fineh Hatton Creek; Upper St Helen's Creek, Mt Dalrymple road; Mt William and the Broken River Campground (E.V., sighting only). QMJ49668 is from 'Eungella N.P.' (listed in material examined). This loeality lacks preeision and eneompasses all the above eolleetion sites. The eore habitat is eentred in the rainforests of the Mt William, Mt David and Mt Dalrymple eatehments. Two other vertebrates endemic to Eungella are narrowly restrieted to this area: *Eulamprus luteilateralis* and *Rheobatrachus vitelliinus* (K. MeDonald (EPA) pers. eomm.). *E. luteilateralis* is eonfined to altitudes above 900m (Covaeevieh & MeDonald, 1991) and *R. vitellinus* (before its disappearanee in 1985) was found above 400m (MeDonald, 1990).

It is reasonable to projeet a deeline in the quality of rainforest habitat in the Dalrymple Heights as a eonsequenee of global warming. Using projeetions of speeies' distributions for future elimate seenarios (projeeted to 2050), Thomas et al. (2004) assessed extinetion risks for a sample of 1,130 terrestrial speeies (vertebrates, invertebrates and plants) from areas from Mexieo to Australia. Even their minimum projeetions are alarming; 9-13% extinetion where species have no limits to dispersal and 22-31% where they are ineapable of dispersal. The impact of rising temperatures on plant and animal eommunities living in environmental extremes (polar and high altitude) is diseussed in a reeent popular artiele (Montaigne, 2004), aptly titled 'No Room to Run'. Extrapolating from the predietions of Thomas et al. (2004), *Saproscincus eungellensis* and a number of other Queensland reptiles (notably *Calyptotis thorntonensis*, *Eulamprus frerei*, *E. luteilateralis*, *E. tryoni*,

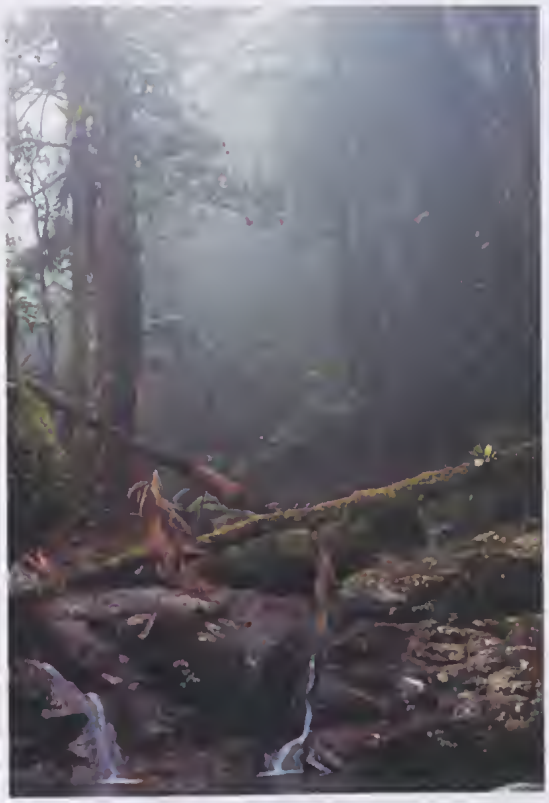

FIG. 5. Habitat of *Saproscincus eungellensis* sp. nov., Finch Hatton Creek.

*Lampropholis robertsi* and *Techmarscincus jigurru*) may have an elevated extinction risk. These lizards all occupy high altitude rainforest refugia and have very limited dispersal capabilities. Whether they can acclimatize to rising temperature cannot be assessed on current knowledge. It is worth noting that the *Saproscincus* spp. so far assessed for mean critical thermal maximum temperature (CTMax) (*S. hannahae* as *Lampropholis* sp. 4 in Greer 1980; *S. mustelinus* and *S. tetradactylus* as *Lampropholis* sp. 5 in Greer 1980) all have a low (CTMax) when compared to other Australian skinks (35.5, 38.6 and 35.3°C respectively; Greer, 1980, 1989).

The upward migration of low and mid altitude plant and animal species in response to global warming threatens the integrity of montane communities. In assessing the affects of climate change on mountain plants, Grabherr et al. (1994) stated that '...the warming is sufficient to stimulate migration, and may cause disastrous extinctions in these environments'.

The forested area at Dalrymple Heights has already been reduced by clearing for dairying (between 1947 and 1962; Brown, 1999) and 2,000 hectares, in State Forest 62, were logged between 1960 and 1976 (Brown, 1999). Rainforest logging totally ceased in this area in 1992 (D. Croker (DPI-Forestry) pers. comm.). 'Many of the most severe impacts of climate-change are likely to stem from interactions between threats,...' (Thomas et al., 2004) and the rainforests of Dalrymple Heights may be particularly prone to damage. In 1975, *Phytophthora cinnamomi* was identified from soil samples taken from dead patches of rainforest at Dalrymple Heights. Brown (1999) stated that 'Area calculations over the most severely affected 641 ha at Dalrymple Heights indicated that, while there were probably no deaths in 1970, by 1976 4.6% of the forest was dead. This increased to 11.9 % in 1978 and further to 19.3% (125 ha in total) in 1980'. At the time of this study, the Dalrymple Heights rainforest patch deaths were reported as '... by far the most severely affected area of rainforest seen

FIG. 6. Habitat of *Saproscincus eungellensis* sp. nov., St Helens Creek.

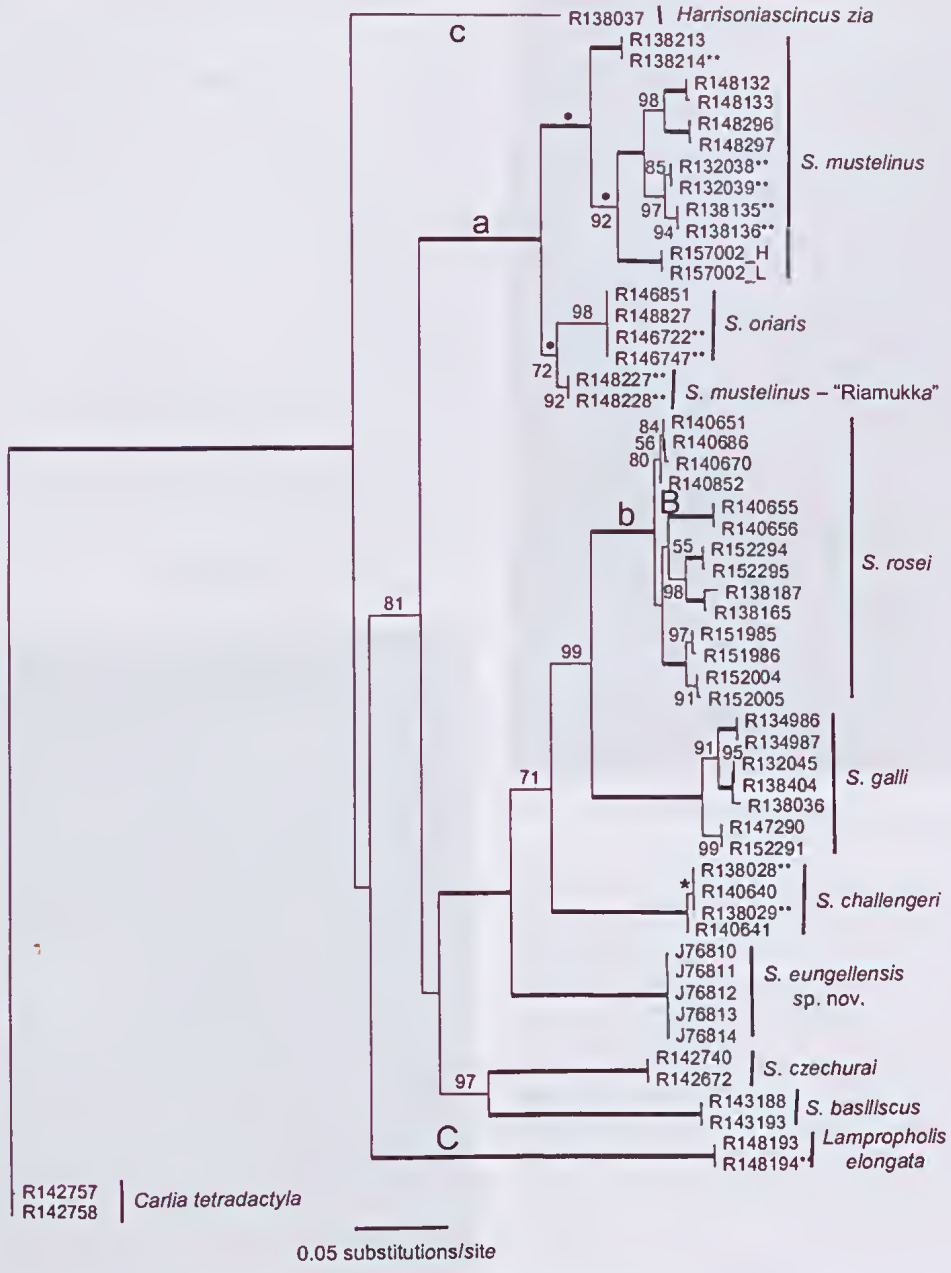


FIG. 7. One of six maximum likelihood (ML) trees for the combined data. The one branch not observed in the strict consensus of the ML trees is indicated by an asterisk. Thicker branches have a posterior probability of 100 percent in Bayesian analyses. Numbers near branches indicate posterior probabilities less than 100 but greater than 50. Thinner branches without figures have posterior probabilities less than 50. Differences from the maximum parsimony (MP) strict consensus topology are indicated. The three branches indicated by dots are not observed in the MP consensus giving a five branch polytomy at "a". Branch "B" in the ML tree is moved to "b" in the MP consensus and branch "C" in the ML tree to "c" in the MP consensus. Two tissues were sequenced from AMS R157002 as an internal control: H = heart and L = liver. Specimens not scored for CytB are indicated with a double asterisk.

from aerial observation, aerial photography and ground inspections anywhere in the tropical rainforests of Queensland' (Brown, 1999). There has been subsequent recovery (while patches of die-off are still present, they do not represent large areas when viewed from above; D. Ball (EPA) pers. comm.) but *P. cinnamomi* remains in the soil and there is evidence that both logging and feral pigs (present in Eungella NP) have played a role in its dissemination (Brown, 1999). A forest stressed by rising temperatures may be vulnerable to future *Phytophthora* outbreaks. *Phytophthora cinnamomi* is active in the soils of Eungella's rainforests during the summer (September-May) when soil temperatures are 20-21° C (Brown, 1999), however, higher temperatures (24-28° C) are optimal for hyphal growth and sporangial production (Cahill, 1999).

INTRAGENERIC RELATIONSHIPS. An independent genetic study of all species in the genus by Moussalli et al. (2005) using a combined ND4 & 16S dataset gave strong support for two clades within *Saproscincus*: a 'northern' and a 'southern' group. The 'northern' group corresponded to the monophyletic lineage of relatively small species defined morphologically by Greer (1989), while the 'southern' group included both the '*mustelinus*' and '*challengeri*' groups (with *S. eungellensis* in the latter) as sister taxa.

Our phylogenetic analysis of representatives of 8 of the 11 species in the genus using portions of the mitochondrial 12S and Cytb genes combined, and both likelihood (maximum likelihood and Bayesian) and maximum parsimony analyses, was able to identify the major groups and clearly identified the '*mustelinus*' group as the sister to the 'northern' group + '*challengeri*' group. Our analyses did identify the two 'northern' group representatives (*S. czechurai* and *S. basiliscus* as sister species, but does not provide strong support for a close relationship between these species and the '*challengeri*' group (Fig. 7).

Both Moussali et al. (2005) and this study clearly identified monophyly of the '*challengeri*' group inclusive of *S. eungellensis*, but differ in the placement of *S. eungellensis* within that clade. The combined ND4 & 16S analysis placed *S. eungellensis* as the sister taxon to the species pair *S. spectabilis* + *S. rosei*, with *S. challengeri* basal within the group. The maximum likelihood and Bayesian analyses for 12S and Cytb combined give moderate support for *S. eungellensis* as the sister taxon to all other species in the '*challengeri*' group (Fig. 7). Genetic difference between the species in the '*challengeri*' group is relatively high with average pairwise Kimura two-parameter distances of 0.128 between *S. eungellensis* and *S. challengeri* (based on 12S data only), and ranges of 0.098 to 0.105 (12S) or 0.111 to 0.143(Cytb) between populations of *S. challengeri* and *S. spectabilis* and 0.064-0.068 (12S) or 0.165 – 0.237 (Cytb) between populations *S. challengeri* and *S. rosei*. The average pairwise distances between populations of *S. spectabilis* and *S. rosei* range between 0.050 and 0.102 (12S) and 0.152 and 0.181 (Cytb). These are relatively deep divergences. Such levels of differentiation between rainforest restricted species in the Wet Tropics of northern Australia have been attributed to vicariance associated with the contraction of rainforests to isolated refugia during the Miocene and Pliocene (Schneider et al., 1998; Schneider & Moritz, 1999; Moritz et al., 2000; & Moussalli et al., 2005).

At a finer scale regional differentiation across the range of the various populations of *S. rosei* was observed, but there is little structure or indication of intrapopulation relationships. This pattern is consistent with a species that has undergone recent widespread range increases from a single source population, possibly as a result of initial contraction to a single refugium with subsequent expansion. Contraction of rainforest during the Pleistocene glacial periods and subsequent expansion during the Holocene has been proposed as the mechanism by which such patterns of low level genetic differentiation are present in now disjunct rainforest blocks in the Wet Tropics (Schneider et al., 1998; Schneider & Moritz, 1999).

Within the '*mustelinus*' group the combined 12S and Cytb ML analysis found posterior probability support of 72% for a sister group relationship between *S. oriaris* and the Riamukka population of *S. mustelinus*. The closeness of the relationship is emphasized by the fact that the Kimura two-parameter genetic distance between these groups averages 0.015 for 12S (Cytb was not scored in the Riamukka population) but ranges between 0.028 and 0.043 for comparisons of Riamukka population and other populations of *S. mustelinus*. However, *S. oriaris* and the northern Tablelands populations of *S. mustelinus* are morphologically distinct and the status of *S. oriaris* as a valid species has not been challenged since its description 5 years ago.

A similar relationship, a sister-group relationship between *S. oriaris* and a 'central' population of *S. mustelinus* (although a different sampling of localities was used) was observed by Moussalli et al (2005), and was attributed to a recent and rapid origin of *S. oriaris* from geographically adjacent populations of *S. mustelinus*.

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## APPENDIX

Specimens used in mitochondrial DNA study with corresponding tissue numbers (in brackets) and locality data.

*Carlia tetradactyla*: AMSR142757 (NR2040), AMSR142758 (NR2041), Mandurama, 4.2km NE at Coombing Creek crossing, NSW, 33°38'S 149°07'E.

*Harrisoniascincus zia*: AMSR138037 (NR621), Border Ranges National Park, vicinity of Brindle Creek rest area, NSW, 28°22'37"S 153°03'14"E.

*Lampropholis elongata*: AMSR148193 (NR3749), AMSR148194 (NR3750), Riamukka State Forest, NSW, 31°19'S, 151°39'E.

*Saproscincus basiliscus*: AMSR143188 (NR2191), Lamb Range, Qld, 17°07'S, 145°36'E; AMSR143193 (NR2192), Lamb Range, Qld, 17°08'S, 145°36'E.

*Saproscincus czechurai*: AMSR142672 (NR2124), Lamb Range, Qld, 17°06'S, 145°34'E; AMSR142740 (NR2101), Lamb Range, Qld, 17°07'S, 145°36'E.

*Saproscincus mustelinus*: AMSR132038 (NR375), AMSR132039 (NR376), Northbridge, Tunks Park, Sydney, NSW, 33°49'S, 151°13'E; AMSR138135 (NR571), AMSR138136 (NR572), Charlestown, Newcastle, NSW, 32°58'S, 151°41'E; AMSR138213 (NR718), AMSR138214 (NR718), Styx River State Forest, Beech Lookout, NSW, 30°31'S, 152°21'E; AMSR148132 (NR2782), AMSR148133 (NR2783), Kanangra Boyd National Park at Hollanders Creek, NSW, 33°50'S, 150°02'E; AMSR148227 (NR3782), AMSR148228 (NR3783), Riamukka State Forest, NSW, 31°20'S, 151°39'E; AMSR148296 (NR3870), AMSR148297 (NR3871), Mount Wilson area, NSW, 33°29'S, 150°25'E; AMSR157002 (NR7752), Murrurundi, NSW, 31°46'S, 150°50'E.

*Saproscincus eungellensis*: QMJ76810-14 - see type information for localities.

*Saproscincus challengeri*: AMSR138028 (NR631), AMSR138029 (NR632), Mount Warning National Park, vicinity of Breakfast Creek, NSW, 28°23'S, 153°17'E; AMSR140640 (NR2000), AMSR140641 (NR2000), Cunninghams Gap, Qld, 28°03'S, 152°25'E.

**MINIMUM CALLING ALTITUDES OF *COPHIXALUS* FROGS ON THORNTON PEAK, NORTHEASTERN QUEENSLAND.** *Memoirs of the Queensland Museum 51(2): 572 2005:-* The mountain-top fauna of the Wet Tropic region of NE Queensland are predicted to be particularly vulnerable to increased temperatures associated with global climate change (Williams et al., 2003). Bioclimatic modelling has revealed the *Cophixalus* frogs to be the most severely threatened vertebrate group in the Wet Tropics (Williams et al., 2003). Future monitoring of the *Cophixalus* frogs requires, amongst other things, knowing the current altitudinal range boundaries of species (Hoskin, 2004; Shoo & Williams, 2004). Many of these range boundaries have recently been clarified (Hoskin, 2004; Shoo & Williams, 2004) compared to earlier estimates (Zweifel, 1985; McDonald 1992), but several gaps remain. In particular the altitudinal range boundaries of the two *Cophixalus* species found on Thornton Peak remain poorly known.

*Cophixalus concinnus* and *C. aenigma* inhabit Thornton Peak. *Cophixalus concinnus* is a high altitude Thornton Peak endemic that is listed as critically endangered under IUCN criteria, due to its limited distribution (estimated to be approx. 7.18 $km^2$ (Hoskin, 2004)) and a predicted rapid population decline due to global warming (Williams et al., 2003). *Cophixalus aenigma* is a vulnerable species distributed across four disjunct upland areas in the northern Wet Tropics (Thornton Uplands, Carbine Uplands, Finnigan Uplands, and possibly Bakers Blue Mountain) (Hoskin, 2004).

We estimated the altitudinal range boundaries of *C. aenigma* and *C. concinnus* on Thornton Peak by determining the location of calling males under ideal conditions on a single night. The survey was achieved by ascending and descending Thornton Peak via the Queensland National Parks and Wildlife Service trail up the southwestern slope from 200 m above seal level (asl) to the summit (1374 m). The starting point of the ascent was at the junction of two tributaries of Hilda Creek (16°11'16"S, 145°21'27"E). The survey was conducted during the night of 12 March 2004. In excess of 150 mm of rain had fallen in the previous two days and rainfall had been high for several weeks preceding. On the night of the survey conditions for calling activity were ideal: rainfall was moderate, wind was essentially absent, and the temperature at 1100m asl was 18°C. The ascent was conducted soon after dark (18:30), when microhylid calling activity is generally greatest (Hoskin, pers. obs.). An hour was spent around 1100m conducting density transects, and descent occurred from 22:00 – 01:00. The altitude of calling males was determined to within 5 m accuracy using a Casio Pathfinder altimeter, which was calibrated at a known altitude at the beginning of the ascent.

The lowest calling *C. aenigma* male was at 700 m asl (16°10'34"S, 145°21'51"E) and this species was abundant between 740–1000 m, and then less commonly heard, but still present, to the summit. The lowest calling male *C. concinnus* was located at 1080 m asl (16°10'11"S, 145°22'01"E) and the species was abundant from 1100 m to the summit. Two surveys of abundance were conducted at approximately 1125 m (16°10'08"S, 145°22'04"E) in which all males calling within 20 m of either side of a 50 m transect were recorded. There were 16 *C. concinnus* and 4 *C. aenigma* recorded on the first transect, and 30 *C. concinnus* and 3 *C. aenigma* on the second. Between the ascent early in the evening and descent several hours later, there was no difference in the altitude of the lowest calling male of both species. The lower altitudinal limits for *C. concinnus* and *C. aenigma* found in this survey are similar to those determined from data lodged with Queensland Museum specimens collected since the 1970's (Hoskin, 2004).

This survey provides an estimate of the altitudinal distribution of each species on a single transect on a single night. Further surveys are required to assess variation in the lower altitudinal limits of the two species on this transect and across other aspects of Thornton Peak. Additionally, estimates of the density of each species across their altitudinal range, as performed by Shoo & Williams (2004) for other *Cophixalus* species, would be valuable for monitoring the impact of global climate change. In conjunction with this, it is important to determine the effect of microhabitat on altitudinal distribution and abundance. In this survey it was evident that *C. concinnus* was particularly common in areas where vegetation grows amongst large jumbled boulders. Such habitat is characteristic of the higher altitudes of Thornton Peak, but does not appear to be the primary determinant of the lower altitudinal limit of *C. concinnus* as apparently suitable boulder habitat occurred below the lowest calling male (1080 m) down to 900m asl. Whether the lower altitudinal limits of the upland *Cophixalus* are determined by thermal tolerance remains untested.

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# A NEW SPECIES OF SPINY-TAILED GECKO (SQUAMATA: DIPLODACTYLIDAE: *STROPHURUS*) FROM INLAND QUEENSLAND

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Sadlier, R.A., O'Mcally, D. & Shea, G.M. 2005 12 01: A new species of Spiny-tailed gecko (Squamata: Diplodactylidae: Strophurus) from inland Queensland. *Memoirs of the Queensland Museum* **51**(2): 573-582. Brisbane. ISSN 0079-8835.

A Spiny-tailed gecko, *Strophurus krisalys* sp. nov., is described from inland areas of Queensland and coastal and near coastal areas in the Gulf of Carpentaria. It has blue mouth colour, enlarged spines above the eye, and parallel rows of enlarged, and uniformly coloured tail spines. In these characteristics it is most similar in morphology to *Strophurus wellingtonae* from inland areas of southern Western Australia, but genetically most similar to the eastern Australian *Strophurus williamsi*. In the north and southeast margins of its range *Strophurus krisalys* is parapatric in distribution with two morphologically different populations of *Strophurus ciliaris*. The new species is arboreal so clearing of native woody vegetation is likely to result in loss and overall fragmentation of populations. □ Strophurus, *Gekkonidae, Queensland, spiny-tail, gecko*.

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*Strophurus* is a morphologically diverse lineage of Australian geckos diagnosed primarily by a character previously considered unique within reptiles: tail glands which produce a viscous substance that is extruded through small rupture sites located on the dorsal surface of the tail (Greer, 1989). Extrusion of glandular secretions from the tail has been reported in the New Caledonian gecko *Eurydactylodes* (Böhme & Sering, 1997), but the mechanism is structurally different and independently evolved.

Greer (1989) identified a small monophyletic species group within *Strophurus* on the basis of small size and lack of femoral pores. The remaining species he regarded as highly divergent in morphology, particularly in scalation, with varying patterns of enlargement of the ciliary, dorsal, and tail scales, forming elongate spines in the most extreme cases. Molecular studies (Melville et al., 2004) identified these as a monophyletic group containing several discrete clades.

Kluge (1967) reviewed the status of *S. ciliaris* (as *Diplodactylus ciliaris*), identifying eight discrete and largely allopatric forms distributed through inland and northern Australia. Kluge identified five populations of *S. ciliaris* with unicoloured tail spines: 'population 3' from southern NT and northern SA; 'population 4' from central northern SA; 'population 6' from inland central Qld; 'population 7' from southwest Qld; and 'population 8' from inland southern WA. Kluge did not record the species from NSW, although it has since been reported from the northwest of the state (Swan et al., 2004), and the NSW material agrees with Kluge's 'population 7' (pers. obs.), and closes the gap between the Qld material referable to 'population 7' and Kluge's 'population 4' in northeast SA.

Storr (1988) reviewed *D. ciliaris* in WA and recognised three of Kluge's 'populations' and a putative hybrid zone in the west of the continent as species and subspecies: 'population 8' was described as *Diplodactylus wellingtonae*; the hybrid zone between 'population 5' and *S. intermedius* as *D. assimilis*; and 'population 1' and 'population 5' as *D. ciliaris ciliaris* and *D. ciliaris aberrans* respectively.

The status of *S. ciliaris* outside of WA has not been reviewed since Kluge (1967). We focus on the population of *Strophurus* formerly identified as 'population 6' (Kluge, 1967) from Qld using both morphological and genetic data, and described here as *S. krisalys* sp. nov.

## MATERIALS AND METHODS

Specimen abbreviations: Specimen abbreviations are prefixed as follows: Australian Museum, Sydney (AMS); Queensland Museum, Brisbane (QM); Western Australian Museum, Perth (WAM); South Australian Museum, Adelaide (SAM); and Northern Territory Museum, Darwin (NTM).

MORPHOLOGICAL ANALYSIS. The main diagnostic characters used are features of tail scalation, and the description and table are based on individuals with complete tails that could be scored for these characters. On these specimens the morphological characters listed below were scored where possible (bilateral scalation characters were scored on both sides and the mean value used).

Measurements: snout to vent length (SVL) - tip of snout to anterior margin of vent; head length – tip of snout to posterior extreme of lower jaw, expressed as a percentage of snout to vent length; head width – width of jaw measured at labials below mid-orbit, expressed as a percentage of head length; snout length – tip of snout to anterior edge of orbit, expressed as a percentage of head length; hindlimb length – groin from apex of crease to tip of fourth toe, excluding claw, expressed as a percentage of snout to vent length; tail length - measured from posterior margin of vent to tip of tail, on complete original tails only, expressed as a percentage of snout to vent length.

Scalation: rostral crease – mid-dorsal groove either partially or completely dividing rostral scale (enlarged scale covering tip of snout), length of groove relative to total height of rostral scale; nasal – number of enlarged scales separating rostral from anterior margin of nostril; supranasal – number of enlarged scales bordering superior margin of nostril; postnasal – number of scales bordering posterior margin of nostril; internasal – number of scales between right and left anterior nasals, immediately posterior to rostral; upper labials – number of enlarged scales bordering upper margin of lip, from rostral to immediately below mid-orbital level; snout scales – number of scales in a longitudinal row from centre of skull at mid-orbit to (and including) scale adjacent to rostral (internasal); interorbitals – number of scales in transverse row across the skull between enlarged ciliaries at mid-orbit; supraciliary – number of enlarged spinose scales projecting beyond margin of dorsal eyelid at its posterior margin; apical plates – the enlarged scales covering terminal underside of digit; fourth finger and toe lamellae – number of scales comprising much enlarged transverse scales on underside of digits (Kluge's secondaries) proximal to apical plates, and number of elliptical or round scales (in pairs) proximal to enlarged transverse scales to emergence of digit (Kluges tertiaries); tail spines – number of enlarged scales on dorsal surface of tail in regular longitudinal rows, counted from posterior extreme of cloacal swelling to tip of tail; intercaudals – number of scales in a transverse line across tail between longitudinal rows of caudal spines, counts taken at mid-tail length at row posterior to that bordering anterior edge of caudal spine; outercaudals - number of scales in a transverse line across the underside of the tail between longitudinal rows of caudal spines, counts taken at mid-tail length at row posterior to that bordering anterior edge of caudal spine; intracaudals - number of scales between (but not including the caudal spines of same longitudinal row, counts taken from caudal spine at mid-tail length to next spine immediately posterior; preanal pores – external openings of preanal glands in scales anterior to the vent, and are given as separate values for the left and right sides, counts are for males only; interpore scale – number of scales interrupting the preanal pore series on midline.

DNA EXTRACTION AND SEQUENCING. Samples of those taxa identified as being morphologically similar to the new species were (*S. ciliaris* 'population 7' and *S. wellingtonae*) were included in the genetic analysis using mitochondrial DNA sequences. This comparison was extended to include other populations currently included under *S. ciliaris*, and species from adjacent regions (*Strophurus williamsi*) that might have affinities with, or be confused with, the new species. An individual of *Oedura tryoni* was selected as the outgroup for other diplodactyline taxa.

DNA was extracted from frozen or ethanol-fixed tissue samples using a modified protocol of Saghai-Maroof et al. 1984). About 0.2g of tissue was placed in 600µL 2× C-TAB buffer (100mM Tris; 1.4M NaCl; 20mM EDTA; 2% hexadecyltrimethylammonium bromide (C-TAB); and 2% 2-β-mercaptoethanol). For all samples, 20µL of Proteinase K (20mg/mL) (Amresco) was added and the samples homogenised in microfuge tubes with a plastic pestle. After an overnight incubation at 37°C or two to three hours at 65°C, one volume of phenol:chloroform:isoamyl alcohol (24:24:1 *v/v/v*) (Sigma) was added, the tubes mixed by inversion and centrifuged at maximum speed for two minutes in an Eppendorf 5154D microfuge. The upper aqueous layer was removed to a fresh tube containing one volume of chloroform:isoamyl alcohol (24:1 *v/v*) (Amresco). The tubes were again mixed by inversion and centrifuged for two minutes at maximum speed. The aqueous layer was then removed to a fresh tube containing one volume of isopropanol. The tubes were inverted several times and stored

overnight at –20°C. After centrifuging for thirty minutes at maximum speed, the supernatant was removed and 500µL of 70% ethanol added to wash the DNA pellet. After brief vortexing, and a final spin for ten minutes at maximum speed, the supernatant was removed and the pellet dried under vacuum for five minutes. Depending on the size of the pellet, gauged by visual inspection, the DNA was resuspended in 100µL TE (0.1M Tris, 0.01M EDTA). The amount and quality of DNA was estimated by agarose gel electrophoresis (Sambrook et al., 1989)

Partial sequences of the protein encoding mitochondrial gene for Cytochrome *b* (cyt *b*) and partial sequences for mitochondrial 12S and 16S rDNA genes were obtained. Primer pairs L14841 and H15149 (Kocher et al., 1989) amplified a 307bp fragment of cyt *b*, excluding the primer sequences. The primer pairs L1091 and H1478 (Kocher et al., 1989) amplified a 361bp fragment of the 12S rDNA gene. The primer pairs 16SLF: 5'- CGC CTG TTT ATC AAA AAC AT -3' and 16SHR: 5'- CCG GTC TGA ACT CAG ATC ACG T-3' (H. Lui, pers. comm.) amplified a 507bp fragment of the 16S rDNA gene.

Polymerase chain reaction (PCR) conditions were the same for all primer sets. Amplifications were carried out in 25µL volumes containing 1.5 mM $MgCl_2$, 0.025mM of each dNTP, 12.5pmol of each primer, 0.2U of Qiagen *Taq* DNA polymerase, 2.5µL of Qiagen 10× PCR buffer and 1 – 100ng of whole genomic DNA (generally a 1:20 – 1:50 dilution of the stock DNA extraction). A negative control (containing no template DNA) was included for each batch of amplifications. The following cycling profile was used for all experiments: an initial denaturation at 94°C for one minute, then 30 cycles of 94°C for 20 secs, annealing for 30 secs (50°C for cyt *b* and 52°C for 12S and 16S rDNA genes), extension at 72°C for 1½ minutes, and a final extension at 72°C for 2 mins. PCRs were checked for success by running 5µL of the reaction on a 2% agarose gel.

PCRs were purified using QIAquiek spin columns (Qiagen). Both forward and reverse strands were sequenced using ¼ volume BigDye version 3 Dye Terminator premix (ABI) with the same primers used for the PCR, according to the manufacturer's instructions. The samples were run on an ABI 310 Genetic Analyser. Forward and reverse strands were combined and sequences checked for errors using the computer program Sequencher (Genecodes). Each cyt *b* sequence was examined to establish the absence of stop codons (the presence of which would indicate a pseudogene or nuclear copy); regions of uncertain alignment of ribosomal genes were excluded from the analysis.

Each gene was aligned first with the computer package ClustalW (Thompson et al., 1994) and then combined and adjusted manually with the Se-Al computer package (Rambaut, 2002). The final alignment consisted of 1185 bases. Regions of ambiguous alignment in the ribosomal DNA genes were excluded. To test for incongruence of phylogenetic signal between the three genes, an ILD test (Farris et al., 1994) was performed in the test version 4.0b10 of PAUP* (Swofford, 2000) therein implemented as a Partition Homogeneity Test.

Genetic distances were calculated using the computer program MEGA version 3.0 (Kumar et al., 2004). The log-determinant (LogDet) distance measure of (Steel 1993) was used, which allows for heterogeneous rates among lineages. Trees were constructed with PAUP* using distance (minimum evolution, ME), maximum parsimony (MP) and maximum likelihood (ML) as the optimality criterion. In each case, the shortest tree was found using a heuristic search with 50 replicates of random taxon addition so as to avoid the tree search being constrained to locally optimum topologies. In most cases, the shortest tree was found after 35 or fewer replicates. For the ME analysis, LogDet distances were used. MP analyses were conducted using the ACCTRAN character optimisation, MULPARS and TBR branch swapping options in PAUP*, as were ML analyses except NNI branch swapping was used. The software program ModelTest v 3.06 (Posada & Crandall, 1998) was used to select parameters of a TnR+Γ+*I* likelihood model. Gaps and uncertainties were treated as missing data and all positions were of equal weight. Branch support was assessed for both ME and MP trees with 1000 bootstrap pseudoreplicates (Felsenstein, 1985). For calculation of bootstrap proportions, heuristic searches were carried out as above, but with 35 random addition replicates. ML bootstrap proportions were calculated over 100 pesudoreplicates, with 3 random taxon addition replicates.

The sequences from this study are available on GenBank under accession numbers AY583930-AY583957 for cyt *b*, AY583856-AY383883 for 12S rDNA and AY583903-AY583929 for 16S rDNA.

Table 1. Comparative table of key body measurements and tail scalation for *Strophurus krisalys* sp. nov., *S. wellingtonae*, and *S. ciliaris* 'population 7' from NSW and Qld.

| | *S. krisalys* sp. nov. | *S. wellingtonae* | *S. ciliaris* 'population 7' |
|---|---|---|---|
| Maximum SVL(mm) | 70.0 | 82.0 | 77.0 |
| Tail length (%SVL) | | | |
| Range | 58.6 – 75.9 | 64.1 – 79.4 | 59.7 – 72.3 |
| Mean | 66.8 | 72.0 | 66.8 ± 0.4 |
| N | 28 | 15 | 18 |
| Caudal spines | | | |
| Range | 18 – 21 | 18 – 22 | 16 – 22 |
| Mean | 19.4 ± 0.8 | 20.25 ± 1.5 | 19.1 ± 1.2 |
| N | 21 | 16 | 14 |
| Intercaudal scales | | | |
| Range | 8 - 13 | 7 – 11 | 4 – 7 |
| mean±sd. | 9.8 ± 1.3 | 9.25 ± 1.3 | 5.4 ± 0.8 |
| N | 27 | 16 | 19 |
| Outercaudal scales | | | |
| Range | 17 – 26 | 21 – 30 | 21 – 29 |
| mean±sd | 21.5 ± 2.1 | 25.3 ± 2.7 | 25.05 ± 2.65 |
| N | 27 | 16 | 19 |
| Intracaudal scales | | | |
| Range | 5 – 7 | 5 – 7 | 4 – 5 |
| mean±sd | 6.0 ± 0.5 | 5.85 ± 0.8 | 4.6 ± 0.5 |
| N | 25 | 16 | 19 |

## SYSTEMATICS

MORPHOLOGICAL COMPARISONS. There is no obvious difference in adult size or body proportions between *S. krisalys* sp. nov. and the 'eastern' *S. ciliaris* 'population 7', but overall adult body size is greater in *S. wellingtonae* than in *S. krisalys* sp. nov. (Table 1).

Direct comparisons of scalation of *S. krisalys* sp. nov. were made with *S. wellingtonae*, the only other *Strophurus* with a similar tail morphology (elevated number of intercaudal scales), and with the parapatric population of *S. ciliaris* from western New South Wales and inland southern Queensland referable to Kluge's 'population 7' that also has enlarged unicoloured spines on the tail. Differences in several scalation characters were observed between *S. krisalys* and *S. wellingtonae* and *S. ciliaris* 'population 7'. In *S. krisalys* sp. nov. (and *S. ciliaris* 'population 7') the enlarged dorsal tubercules are arranged in two parallel but broken rows on each side of the dorsal mid-line of the body, but are present as only a single row on each side of the dorsal mid-line of the body in *S. wellingtonae*. In *S. krisalys* sp. nov. the longitudinal rows of caudal spines are more widely spaced than in *S. ciliaris* 'population 7', the latter having fewer (almost half the number) of intercaudal scales between the longitudinal rows of caudal spines. There is also a tendency for the rostral groove to be complete in most *S. ciliaris* 'population 7' and *S. wellingtonae*, whereas it is incomplete over a third or more the height of the rostral in *S. krisalys* sp. nov..

For those other populations of *S. ciliaris* with unicoloured tail spines Kluge (1967) gave counts for the number of intercaudal scales that clearly diagnosed those populations as having a much lower number of intercaudals ('population 3' 4-5; 'population 4' 3-5) than *S. krisalys* sp. nov. (8-13). The remaining populations of *S. ciliaris* identified by Kluge, including the nominate population (Kluge's 'population 1'), have a mixture of light and dark coloured caudal spines of varying size, readily distinguishing these populations of *S. ciliaris* from *S. krisalys* sp. nov.

MITOCHONDRIAL DNA. The final alignment consisted of 1185 bases: 507 16S, 371 12S and 307 cyt *b*. Three regions of uncertain alignment in the 16S sequence were excluded from phylogenetic analyses (positions 221-256, 318-320 and 375-377 inclusive). Of the remaining nucleotides, 883 were invariant and 202 were parsimony informative. Twelve equally parsimonious trees were recovered, differing only in the branching order within the *S. ciliaris aberrens* clade. Hierarchical likelihood ratio tests using MODEL TEST suggested the use of a TnR+$\Gamma$ +*I* model with the following parameters: base frequencies A=0.3421, C=0.2712, G=0.1566, T=0.2301; substitution rates A↔C=1, A↔G=10.3119, A↔T=1, C↔G=1, C↔T=13.0334, G↔T=1; gamma shape parameter ($\alpha$) =0.1815; and proportion of invariant sites =0.2532. A single ML tree was found (-ln*L*=3960.44)

Results from the ILD test indicated that there was no significant incongruence between the three datasets (p=0.07, $\alpha$=0.1), although the 16S dataset produced polytomies in the distal nodes of the tree. In all analyses of the combined data set (ME, MP & ML), each species was recovered as a monophyletic clade with high bootstrap support (most 100%, with *S. ciliaris* ranging from 92% in the MP analysis (Fig. 1) to 96% in the ME analysis). The combined analysis of all three genes clearly identified *S. krisalys* as a

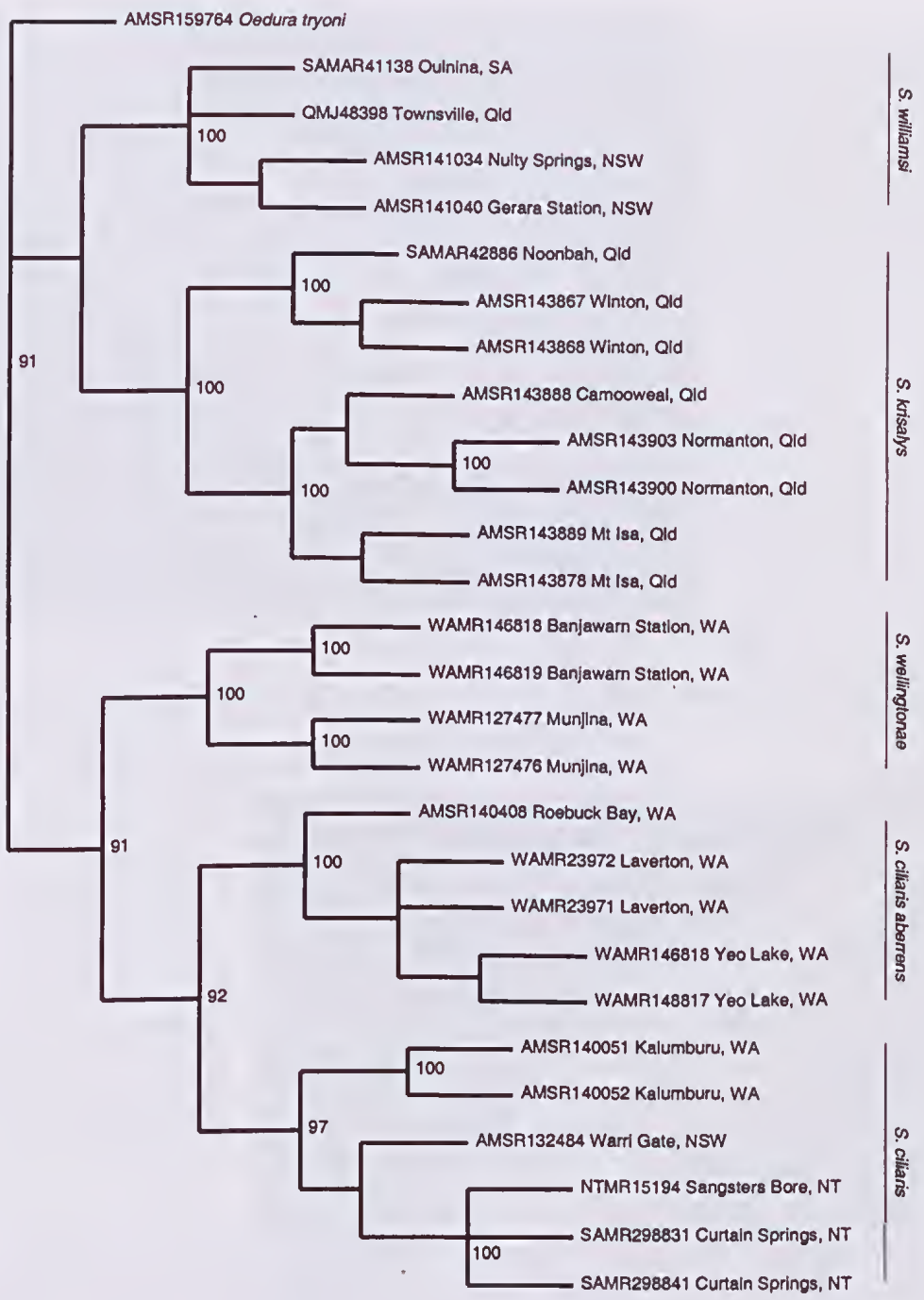


FIG. 1. Maximum parsimony tree of the combined 16S (507 bases), 12S (371 bases) and Cyt b (307 bases) alignment (total length 1185 bases). Bootstrap support was calculated from 1000 replicates of heuristic searches (35 random taxon addition replicates) and is indicated at nodes with values greater than 90%. Maximum likelihood and distance based methods produced similar trees, differing only in the arrangement of individuals from the northern *S. krisalys* sp. nov. population.

distinct group closer to *S. williamsi* than to *S. wellingtonae* or *S. ciliaris*, though bootstrap support for this relationship is unremarkable. Between analyses, the sole topological difference is found between the three northern populations of *S. krisalys*, where the arrangement of individuals is only partially resolved in the ML and ME trees, though bootstrap support varies across all trees (not shown).

Amongst the in-group species, the net distances (Table 2) range from: 0.065 between *S. ciliaris* and *S. wellingtonae*; 0.097 between *S. krisalys* sp. nov. and *S. williamsi*; and 0.109 between *S. krisalys* sp. nov. and *S. wellingtonae*. Within *S. ciliaris*, the subspecies *aberrans* is separated from other *ciliaris* by an average net LogDet distance of 0.053. Within *S. krisalys* sp. nov. a southern group (Noombah and Winton) and a northern group (Mt Isa, Camooweal, and Normanton) separated by a net LogDet distance of 0.044 was found in the combined analysis.

Melville *et al.* (2004) and O'Meally (2004) examined the phylogenetic relationships of *Strophurus*, including *S. williamsi*, *S. wellingtonae* and *S. ciliaris*, among others. In these studies *S. wellingtonae* is a member of the clade that includes *S. ciliaris* and *S. ciliaris aberrans*, and *Strophurus williamsi* a member of a clade that is sister to *S. intermedius*, *S. rankini* and *S. spinigerus*. O'Meally (2004) identified the sister relationship of *S. williamsi* and *S. krisalys* sp. nov. Melville *et al* (2004) reported uncorrected sequence divergences between *S. williamsi* and *S. wellingtonae* of 0.13; *S. ciliaris* of 0.11; and *S. ciliaris aberrens* of 0.11. The topologies and divergences observed are similar to those found in this study and suggest further genetic comparisons of *S. krisalys* sp. nov. with other members of the genus are not warranted.

TABLE 2: Net genetic distances (LogDet) between species included in the mitochondrial DNA analysis.

| | 1 | 2 | 3 | 4 | 4a | 4b | 6 |
|---|---|---|---|---|---|---|---|
| *S. krisalys* sp. nov. (1) | - | | | | | | |
| *S. williamsi* (2) | 0.097 | - | | | | | |
| *S. wellingtonae* (3) | 0.109 | 0.088 | - | | | | |
| *S. ciliaris* all samples (4) | 0.080 | 0.088 | 0.065 | - | | | |
| *S. ciliaris aberrens* (4a) | 0.125 | 0.110 | 0.087 | - | - | | |
| *S. ciliaris* (4b) | 0.114 | 0.097 | 0.074 | - | 0.053 | - | |
| *O. tryoni* (6) | 0.167 | 0.154 | 0.159 | 0.142 | 0.158 | 0.154 | - |

TAXONOMIC CONCLUSIONS. It is clear from the genetic data that Kluge's *S. ciliaris* 'population 6' is not conspecific with *S. ciliaris* sensu stricto but closer to the geographically close *S. williamsi*. It is both morphologically and genetically distinct from *S. ciliaris ciliaris* and from *S. ciliaris* 'population 7', which are the geographically closest populations of *S. ciliaris*; from *S. wellingtonae*, which it most closely resembles morphologically; and from *S. williamsi*. Hence, it is described here as a new species:

**Strophurus krisalys** sp. nov.
(Figs 2, 3)

MATERIAL EXAMINED. HOLOTYPE. QMJ82269 (formerly AMSR143890) 15.6km W of Leichhardt River crossing at Mt Isa on Barkly Hwy, 20°35'S 139°28'E. PARATYPES: *Longreach & Winton District* – AMS R143866-68, QMJ82274-75, 22°19'S 142°43'E. *Mt. Isa & Camooweal District* – AMSR143875, on Boulia road, 20°52'S 139°27'E; AMSR143876-77, on Boulia road, 20°45'S 139°29'E; AMSR143878, on Boulia road, 20°44'S 139°29'E; AMSR143879, on Boulia road, 20°44'S 139°29'E; AMSR143883, on Barkly Hwy, 20°00'S 138°34'E; AMSR143889, on Barkly Hwy, 20°26'S 139°24' E; AMSR143884-85, R143888, QMJ82270-71 on Barkly Hwy, 19°57'S 138°25'E; QMJ71634-35 on Boulia road, 20°45'S 139°29'E. *Normanton & Croydon District* – AMSR63394 Normanton, 17°42'S 141°04'E; AMS R63482-84 Normanton, 17°40'S 141°04'E; AMS R63512-5 Normanton, 17°40'S 141°04'E; AMSR63573, Normanton 17°40'S 141°04'E; QM J82272, Normanton, 17°41'S 141°03'E; AMSR143900 Normanton, 17°42'S 141°02'E; QMJ82273, Normanton, 17°44'S 141°02'E; AMS R143908 Normanton , 17°47'S 141°00'E; AMSR143902 Normanton , 17°48'S 141°00'E; AMSR143903 Normanton , 17°50'S 140°59'E; AMS R143904, Normanton , 17°51'S 140°58'E; AMSR143906 Normanton , 17°52'S 140°57'E.

The type series was chosen from areas represented by specimens used in the genetic study. The registration numbers and corresponding tissue numbers (bracketed) for the specific individuals used in the analyses are as follows: AMSR143866 (NR2365); AMSR143867 (NR2366); AMSR143878 (NR2370); AMSR143888 (NR2458); AMSR143889 (NR2459); AMSR143900 (NR2378); AMSR143903 (NR2377).

DIAGNOSIS. *Strophurus krisalys* can be distinguished from other members of the genus

FIG. 2. *Strophurus krisalys* sp. nov. (AMSR143902) from near Normanton, Qld.

(as defined by Greer, 1989) by its moderately large size, maximum snout to vent length 70.0mm; two rows of enlarged tubercules each side of the dorsal mid-line of the body; a single row of enlarged, spinose tubercules on either side of the tail; spinose scales of tail unicoloured; mouth colour deep blue.

Of species likely to be confused with *S. krisalys* only *S. ciliaris* 'population 7' and *S. wellingtonae* have a single row of enlarged, unicolored, spinose, tubercules on either side of the tail. *S. krisalys* can be distinguished from these species as follows: from parapatric *S. ciliaris* 'population 7' by the deep blue (*vs* yellow) mouth colour and greater number of intercaudal scales (8-13 *vs* 4-7); from *S. wellingtonae* by two parallel rows of enlarged tubercules each side of the dorsal mid-line of the body (*vs* a single row each side of the dorsal mid-line of the body), and partially (*vs* completely) divided rostral scale.

It is distinguished from the genetically closest species *S. williamsi* by having a single (*vs* double) row of enlarged, unicolored, spinose, tubercules on either side of the tail.

ETYMOLOGY. For Kristin Alys Sadlier (krisalys).

DESCRIPTION. *Measurements*: SVL and Tail length given in Table 1; head length 22.1-25.9%.of body length (=24.0%, n=29); head width 60.0-72.5% of head length (=65.6%, n= 29); snout length 40.0-45.6% of head length ( = 42.6%, n = 29).

FIG. 3. *Strophurus krisalys* sp. nov. (AMSR143869) from near Winton, Qld.

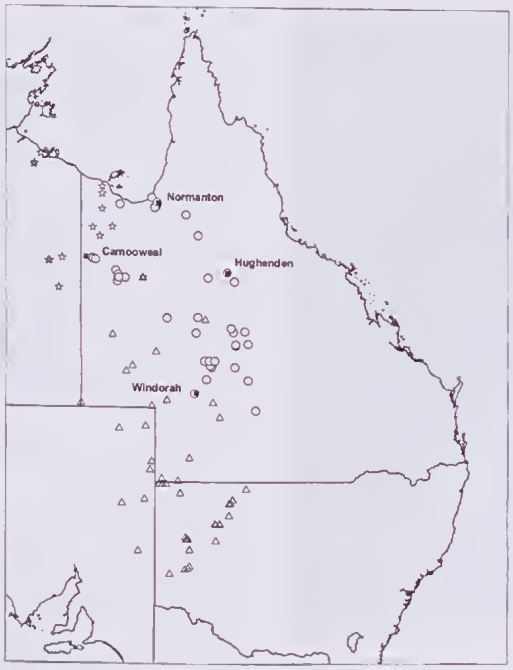


FIG. 4. Distribution map showing museum records for *Strophurus krisalys* sp. nov. (open circle); *S. ciliaris sensu stricto* (open star); and *S. ciliaris* 'population 7' (open triangle).

*Scalation*: Nostril surrounded by rostral, single supranasal, single postnasal, and first labial. Median groove of rostral up to two thirds height of the scale. Internasals 1-3. Upper labials 8-11 ( = 9.4 ± 0.7, n = 29). Interorbitals 25-32 ( = 28.6 ± 1.6, n = 26). Upper margin of eye with 1-3 enlarged ciliary spines, posterodorsal margin 1-2 smaller ciliary spines. Underside of digits of forelimbs with single pair of large apical plates, followed on fourth digit by 4-5 transverse lamellae and proximally by 0-3 pairs of elliptical or circular scales. Underside of digits of hind limbs with pair of large apical plates, followed on fourth digit by 3-5 transverse lamellae and proximally by 0-2 pairs of elliptical or circular scales. Preanal pore row in males discontinous, 3-7 on left and 4-7 on right side, and separated by up to 4 scales lacking pores.

Dorsal tubercules arranged as two parallel rows each side of the dorsal mid-line of the body, tending to be widely spaced and scattered posteriorly. Enlarged, spinose, tubercules of tail arranged as a longitudinal row of 18-21 ( = 19.4 ± 0.8, n = 21) spines on either side of the tail, at mid-distance along tail parallel rows are separated transversely by 8-13 ( = 9.85 ± 1.3, n = 27) homogenous flat intercaudal scales and 17-26 ( = 21.5 ± 2.1, n = 27) outercaudal scales, and along each row the spines at mid-distance along tail are separated longitudinally by 5-7 ( = 6.0 ± 0.5, n = 25) intracaudal scales.

*Colour and Pattern*. Specimens from the far north of the species range in the Gulf of Carpentaria usually have a vertebral pattern of well-defined and contrasting dark transverse ellipses which contact medially along the vertebral margin (Fig. 2). Some well marked individuals also have a lateral extension of these dark blotches present as hourglass shaped blotches on the side of the body. The dark dorsal pattern is reduced in two specimens; one is nearly uniformly grey. Specimens from further south have a higher proportion of uniformly coloured individuals (Fig. 3) in the samples.

DISTRIBUTION. Inland Queensland from Windorah and Ambathala in the south through to Normanton in the north, and west to Camooweal (Fig. 4). It is parapatric in distribution with *S. ciliaris* 'population 7' over much of its distribution in the south and southwest, but both species are recorded in the Winton region and sympatry between the two species could be wider than the available samples indicate. In the north of its distribution it is broadly parapatric with *S. ciliaris* sensu stricto.

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## Appendix

ADDITIONAL MATERIAL EXAMINED: Specimens of *Strophurus krisalys* sp. nov.*, *S. ciliaris* 'population 7', and *S. wellingtonae* marked with an asterisk were used in compiling Table 1. Specimens used in the genetic study are marked with a superscript [1]; tissue collection numbers are indicated in brackets. Specimens used in compiling the distribution map (Fig. 4) are also listed.

*Strophurus krisalys* sp. nov. – additional material examined but not included in type series: QMJ312 Normanton, 17°40'S 141°04'E; AMSR52690-91 Karumba, 17°29'S 140°50'E; QMJ28187 Normanton, 17°40'S 141°04'E; AMSR20800 Burketown, 17°45'S 139°33'E; AMSR63613 8.1km W Croydon P.O., 18°09'S 142°13'E; QMJ47535 Esmeralda 19°00'S 142°44'E; AMSR72045 Camooweal, 19°58'S 138°29'E; QMJ24480 Hughenden, 20°31'S 143°54'E; QMJ39030 Mt Isa, 20°43'S 139°31'E; AMSR15138, R26009, R27331-32, R28417-23, R28443, R28448-49, R50738, R64840 Mt Isa, 20°44'S 139°29'E; QMJ30337 Mt Isa, 20°44'S 139°29'E; QMJ31546 Richmond, 20°44'S 143°08'E; AMSR60284 Cloncurry, 20°44'S 139°47'E; AMSR142963 Middleton, 22°21'S 141°28"E; QMJ49968 Acacia Downs, 22°47'S 144°04'E; QMJ57232 Crossmoon Stn, 22°54'S 144°37'E; QMJ8540 Darriveen Stn, 22°56'S 144°10'E; QMJ29124 Mt. Cameron Stn, 22°58'S 142°39'E; QMJ9563 Currane, 23°24'S 144°45'E; QMJ15334 Hughenden, 20°51'S 144°12'E; QMJ54614 Longreach, 23°27'S 144°15'E; QMJ58757 Longreach, 23°26'S 144°15'E; QMJ30324, QMJ32589, QMJ37672, Longreach, 23°26'S 144°15'E; QMJ49796 Longreach, 23°26'S 144°15'E; QMJ52596 Noonbah airstrip, 24°05'S 143°01'E; QMJ58758 Noonbah, 24°05'S 143°11'E; SAMR42886[1] (C038) Noonbah; QMJ58759 Tarcombe Reserve, 24°06'S 143°24'E; QMJ9660 Stonehenge, 24°21'S 143°17'E; QMJ56844 Waterloo, 24°16'S 143°13'E; QMJ6241 Ruthven, 24°20'S 144°11'E; QMJ7879 Jundah, 24°50'S 143°04'E; QMJ61083-84 Idalia N.P. 24°52'S 144°46'E; AMSR141929-30 Windorah 25.25'S 142.36'E; QMJ35686, QMJ35703 Ambathala N.R., No. 3 Bore, 26°05'S 145°04'E.

*Strophurus ciliaris aberrans* (WA): WAMR146816[1] (JEM 32), WAMR146817[1] (JEM 25) Yeo Lake Road 29°09'S 123°48'E; WAMR23971[1], WAMR23972[1] Laverton; WAMR140408[1] (NR1894), Broome.

*Strophurus ciliaris ciliaris* (WA): AMSR140051[1] (NR1063), R140052[1] (NR1064) McGowens Beach, 14°09'S 126°38'E;

*Strophurus ciliaris ciliaris* ? (NT): SAMR29883[1] (ABTC 4220 = BM044), SAMR29884[1] (ABTC 4220 = BM045) Curtain Springs; NTMR15194[1] (SQ97) Sangsters Bore.

*Strophurus ciliaris ciliaris* (Qld.): QMJ28734, Mornington Is, 16°29'S 139°34'E; QMJ47687 Doomadgee, 17°02'S 138°49'E; QMJ51986 Lawn Hill, 18°42'S 138°28'E; QMJ47683 Doomadgee, 17°19'S 138°49'E; QMJ10727, QMJ10908, QMJ10918 Doomadgee, 17°56'S 138°49'E; QMJ2220 Gregory Downs, 18°39'S 139°15'E; QMJ46853 Riversleigh, 19°02'S 138°45'E; QMJ7536 Cloncurry, 20°42'S 140°30E; QMJ34805-06 Georgina Downs, 21°08'S 137°04'E.

*Strophurus ciliaris* 'population 7' (Qld): QMJ7535 Cloncurry, 20°42'S 140°30'E; QMJ34587 Winton, 22°23'S 143°02'E; QMJ43295 Herbert Downs, 23°02'S 139°18'E; QMJ43320-23 Spring Valley, 23°41'S 141°02'E; QMJ48490 Natan Stn, 28°00'S 142°25'E; QMJ58748 (NR2472) Davenport Downs, 24°15'S 140°05"E; AMSR139808* 32.7km SE Thylungra on Damantina Developmental road (Quilpie-Windorah); AMSR139834* Bedourie, 24°27'S 139°49'E; QMJ26476 Quilpie, 25°53'S 143°25'E; AMSR113246* Simpson Desert, 25°46'S 138°00'E; QMJ26475-76, QMJ26511 Cuddapan Stn, 25°39'S 141°30'E; QMJ41760 Beetoota, Wyeroe Ck., Mt. Leonard Stn, 25°52'S 140°53'E; AMSR32601 Omicron, 28°49'S 141°16'E.

*Strophurus ciliaris* 'population 7' (NSW): AMSR132484*[1] (NR358) Warri Gate, 9.8km N, 28°55'S 141°56'E; AMSR155243, R155396 Sturt National Park, 29°02'S 141°18'E; AMSR155249 Sturt National Park, 29°02'S 141°11'E; AMSR155418 Sturt National Park, 29°01'S 141°27'E; AMSR147602 Thoura, 29°16'S 144°41'E; AMSR90907 Tibooburra, 29°26'S 142°01'E; AMSR130500 Wanaaring, 29°43'S 144°07'E; AMSR130853-54 Wanaaring, 29°42'S 144°09'E; AMSR40456, R40815-6, R41085-86 Goorimpa Station, 30°20'S 144°°01'E; AMSR161531-34, R161543-44, R161554, R162658 Paroo-Darling National Park, 30°40'S 143°37'E; AMSR161557 R162587, R162629, R162687, R162715 Paroo-Darling National Park, 30°41'S 143°37'E; AMSR161561, R161639 Paroo-Darling National Park, 30°41'S 143°36'E; AMSR162685 Paroo-Darling National Park, 30°43'S 143°28'E; AMSR162710 Paroo-Darling National Park, 30°41'S 143°27'E; AMSR141904 Coolabah tip, 31°02'S 146°43'E; AMSR150157 Mootwingee National Park, 31°12'S 142°15'E; AMSR146259 Mootwingee National Park, 31°17'S 142°18'E;. AMSR146260, R147273 Mootwingee National Park, 31°18'S 142°20'E; AMSR141893 Girilambone tip, 31°15'S 146°54'E; AMSR132985* Wilcannia, 27km - Wanaaring road, 31°22'S 143°28'E; AMSR107243* Menindee caravan park, 32°24'S 142°25'E; AMSR32811 Kinchega National Park, 32°29'S 142°21'E; AMSR121034* Lake Cawndilla, 32°31'S 142°14'E; AMSR138418 S of Broken Hill, 32°43'S 141°36'E; AMSR123947 E of Broken Hill, 31°44'S 142°25'E.

*Strophurus ciliaris* 'population 7' (SA): SAMR14841 Koonchera Dune, 26°47'S 139°33'E; SAMR16815 within 3km of Strathearn, 31°46'S 140°20'E; SAMR25596 Cordillo Downs Stn., 26°42'S 140°37'E; SAMR38247 6km S of Innamincka Bore No. 3, 28°09'S 140°53'E; SAMR39966 14km SW of Innamincka Bore 2, 28°28'S 140°49'E.

*Strophurus wellingtonae* (WA): WAMR8963* Austin Downs, 27°23'S 117°45'E; WAMR21112* 34 miles E Wiluna, 26°40'S 120°46'E; WAMR27216* Wanjarri Station, Kathleen Valley, 27°19'S 120°33'E; WAMR81320* 2km S Capricorn Roadhouse, 22°26'S 119°47'E; WAMR65871* 2.5km N Mt Linden, 29°1'S 122°25'E; WAMR87463* 3km E White Well, 26°5'S 120°06'E; WAMR87484-86* 20km E Millbillillie, 26°37'S 120°3'E; WAMR87491* 26km W Prenti Downs homestead, 26°34'S 122°34'E WAM105548* 27km S Leonora, 29°06'S 121°21'E; WAMR104489* 42km W Newman, 23°12'S 119°19'E; WAMR127476[1] (W12) & WAMR127477[1]* (W14) Minjina Roadhouse, 22°33'S 118°3'E; WAMR146818[1] (JEM30); WAMR146819[1] (JEM29) Banjawarn Station, 27°36'S 121°40'E.

*Strophurus williamsi*: AMSR141039[1] (NR1292) Nulty Springs, New South Wales; AMSR141040[1] (NR1293) Gerara Station, NSW; QMJ48398[1] (ABTC16229) Townsville, Qld; SAMR41138[1] (ABTC39708) Oulnina SA.

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# CONTENTS

PART 1 (Issued 31 May 2005)

BOLES, W.E.
*Platalea subtenuis* De Vis (Aves)is a White Ibis ..... 1

BURROW, C.J. & YOUNG, G.C.
The acanthodian fauna of the Cravens Peak Beds (Early to Middle Devonian), western Queensland ..... 3

HILLER, N. & MANNERING, A.A.
A new elasmosaurid plesiosaur (Sauropterygia) from the Upper Haumurian (Maastrichtian) of the South Island, New Zealand ..... 27

HOCKNULL, S.A.
Ecological succession during the late Cainozoic of central Queensland: extinction of a diverse rainforest community ..... 39

PLEDGE, N.S.
A new species of Oligocene cetacean from Port Wilunga, South Australia ..... 123

PLEDGE, N.S.
The Riversleigh ?wynyardiids ..... 135

PRICE, G.J. & SOBBE, I.H.
Pleistocene palaeoecology and environmental change on the Darling Downs, southeastern Queensland, Australia ..... 171

REED, E.H. & HUTCHINSON, M.N.
First record of a giant varanid (Megalania, Squamata) from the Pleistocene of Naracoorte, South Australia ..... 203

SCANLON, J.D.
Australia's oldest known snakes: Patagoniophis, Alamitophis, and cf. Madtsoia (Squamata: Madtsoiidae) from the Eocene of Queensland ..... 215

TURNER, S.
Heber Albert Longman (1880-1954), Queensland Museum scientist: a new bibliography ..... 237

WORTHY, T.H.
A new species of Oxyura (Aves: Anatidae) from the New Zealand Holocene ..... 259

NOTES

HOCKNULL, S.A.
Additional specimens of *Bohra* (Marsupialia: Macropodidae) from the Pliocene of Queensland ..... 26

HOCKNULL, S.A.
Late Pleistocene-Holocene occurrence of *Chaeropus* (Peramelidae) and *Macrotis* (Thylacomyidae) from Queensland ..... 38

PRICE, G.J. & HOCKNULL, S.A.
A small adult *Palorchestes* (Marsupialia, Palorchestidae) from the Pleistocene of the Darling Downs, southeast Queensland ..... 202

PART 2 (Issued 31 December 2005)

ARNOLD, P.W., BIRTLES, R.A., DUNSTAN, A., LUKOSCHEK, V. & MATTHEWS, M.
Colour patterns of the dwarf minke whale *Balaenoptera acutorostrata* sensu lato: description, cladistic analysis and taxonomic implications ..... 277

ARNOLD, P.W., BIRTLES, R.A., SOBTZICK, S., MATTHEWS, M. & DUNSTAN, A.
Gulping behaviour in rorqual whales: underwater observations and functional interpretation ..... 309

BRUCE, A.J.
Pontoniine shrimps from Papua New Guinea, with designation of two new genera, *Cainonia* and *Colemonia* (Crustacea: Decapoda: Palaemonidae) ..... 333

BRUCE, A.J.
Note on a new species of *Bresilia* (Crustacea: Decapoda: Bresiliidae) from Zanzibar ..... 385

COOK, A.G. & NÜTZEL
New Devonian gastropods from the Broken River and their palaeoecology ..... 391

CORNELIUS, P.F.S., FENNER, P.J. & HORE, R.
*Chiropsalmus maculatus* sp. nov., a cubomedusa from the Great Barrier Reef ..... 399

DALL, W.
The Penaeoidea (Crustacea: Decapoda) of the NORFANZ Cruise ..... 407

DETTMANN, M.E. & CLIFFORD, H.T.
Fossil fruit of the Grevilleeae (Proteaceae) in the Tertiary of eastern Australia ..... 423
EWART, A.
New genera and species of small ticking and 'chirping' cicadas (Hemiptera: Cicadoidea: Cicadidae) from Queensland, with descriptions of their songs ..... 439
GERSHWIN, L.
*Carybdea alata* auct. and *Manokia stiasnyi*, reclassification to a new family with description of a new genus and two new species ..... 501
KYNE, P.M., JOHNSON, J.W., WHITE, W.T. & BENNETT, M.B.
First records of the False Catshark, *Pseudotriakis microdon* Capello, 1868, from the waters of eastern Australia and Indonesia ..... 525
RAVEN, R.J. & WISHART, G.
The trapdoor spider *Arbanitis* L. Koch (Idiopidae: Mygalomorphae) in Australia ..... 531
SADLIER, R.A., COUPER, P.J., COLGAN, D.J., VANDERDUYS, E. & RICKARD, E.
A new species of scincid lizard, *Saproscincus eungellensis*, from mid-eastern Queensland .... 559
SADLIER, R.A., O'MEALLY, D. & SHEA, G.M.
A new species of Spiny-tailed gecko (Squamata: Diplodactylidae: *Strophurus*) from inland Queensland ..... 573

NOTES

FRANKLIN, T. & BURNS, D.
A Southern Right Whale, *(Eubalaena australis)*, in Hervey Bay, Qld and Ballina, N NSW ..... 308
COOK, A.G. & STILWELL, J.D.
Fossil limpet from the Cretaceous of north Queensland ..... 398
COOK, A.G.
First record of fossil freshwater gastropods within the Winton Formation ..... 406
SHEA, G.M.
The type locality of the Sphagnum Frog *Philoria loveridgei* (Anura: Myobatrachidae) ..... 524
ENGEL, M.
A new sawfly from the Triassic of Queensland (Hymenoptera: Xyelidae) ..... 558
HOSKIN, C.J. & HIGGIE, M.
Minimum calling altitudes of *Cophixalus* frogs on Thornton Peak, northeastern Queensland .. 572

S1163

NOTES

FRANKLIN, T. & BURNS, D.
A Southern Right Whale, (*Eubalaena australis)*, in Hervey Bay, Qld and Ballina, N NSW. . . . 308
COOK, A.G. & STILWELL, J.D.
Fossil limpet from the Cretaceous of north Queensland . . . . . 398
COOK, A.G.
First record of fossil freshwater gastropods within the Winton Formation . . . . . 406
SHEA, G.M.
The type locality of the Sphagnum Frog *Philoria loveridgei* (Anura: Myobatrachidae) . . . . . 524
ENGEL, M.
A new sawfly from the Triassic of Queensland (Hymenoptera: Xyelidae) . . . . . 558
HOSKIN, C.J. & HIGGIE, M.
Minimum calling altitudes of *Cophixalus* frogs on Thornton Peak, northeastern Queensland . . 572

## CONTENTS

ARNOLD, P.W., BIRTLES, R.A., DUNSTAN, A., LUKOSCHEK, V. & MATTHEWS, M.
Colour patterns of the dwarf minke whale *Balaenoptera acutorostrata* sensu lato: description, cladistic analysis and taxonomic implications ..... 277

ARNOLD, P.W., BIRTLES, R.A., SOBTZICK, S., MATTHEWS, M. & DUNSTAN, A.
Gulping behaviour in rorqual whales: underwater observations and functional interpretation .. 309

BRUCE, A.J.
Pontoniine shrimps from Papua New Guinea, with designation of two new genera, *Cainonia* and *Colemonia* (Crustacea: Decapoda: Palaemonidae) ..... 333

BRUCE, A.J.
Note on a new species of *Bresilia* (Crustacea: Decapoda: Bresiliidae) from Zanzibar ..... 385

COOK, A.G. & NÜTZEL
New Devonian gastropods from the Broken River and their palaeoecology ..... 391

CORNELIUS, P.F.S., FENNER, P.J. & HORE, R.
*Chiropsalmus maculatus* sp. nov., a cubomedusa from the Great Barrier Reef..... 399

DALL, W.
The Penaeoidea (Crustacea: Decapoda) of the NORFANZ Cruise ..... 407

DETTMANN, M.E. & CLIFFORD, H.T.
Fossil fruit of the Grevilleae (Proteaceae) in the Tertiary of eastern Australia ..... 423

EWART, A.
New genera and species of small ticking and 'chirping' cicadas (Hemiptera: Cicadoidea: Cicadidae) from Queensland, with descriptions of their songs..... 439

GERSHWIN, L.
*Carybdea alata* auct. and *Manokia stiasnyi*, reclassification to a new family with description of a new genus and two new species ..... 501

KYNE, P.M., JOHNSON, J.W., WHITE, W.T. & BENNETT, M.B.
First records of the False Catshark, *Pseudotriakis microdon* Capello, 1868, from the waters of eastern Australia and Indonesia ..... 525

RAVEN, R.J. & WISHART, G.
The trapdoor spider *Arbanitis* L. Koch (Idiopidae: Mygalomorphae) in Australia ..... 531

SADLIER, R.A., COUPER, P.J., COLGAN, D.J., VANDERDUYS, E. & RICKARD, E.
A new species of scincid lizard, *Saproscincus eungellensis*, from mid-eastern Queensland.... 559

SADLIER, R.A., O'MEALLY, D. & SHEA, G.M.
A new species of Spiny-tailed gecko (Squamata: Diplodactylidae: *Strophurus*) from inland Queensland ..... 573